Senckenbergiana lethaea | 57 | (2/3) | 87—183 | Frankfurt am Main, 19. 7. 1976

Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany.

Part 5:
Myriapoda and additional forms, with general remarks on fauna and problems regarding invasion of land by arthropods.

With 107 text-figures, 2 tables and 10 plates.

Leif Størmer.

Abstract.

The present part 5 deals with the myriapod *Eoarthropleura devonica* n. g., n. sp., representing a new family. This species of which the head, last segments of the trunk, ventral plates and fragments of appendages are preserved, is evidently related to the Carboniferous *Arthropleura*. — The additional arthropod remains comprise a scorpion, the spider *Archaeometa ? devonica* n. sp. apparently related to a Carboniferous species, the eurypterid *Jaekelopterus rhenaniae*, and previously known species demonstrating new details. At least the majority of the eurypterids preserved probably represent shed moults, some of them showing a characteristic bend of the body, — a current position. — — The mixed flora and fauna of the Nellenköpfchen-Schichten are of considerable palaeobiological interest. The plants indicate water and swamp environments. Certain bivalves were marine (probably enduring also brackish water), one scorpion was evidently aquatic and the small arachnids evidently terrestrial. The eurypterids belonging to the Hughmilleriidae-Stylonuridae assemblage indicate brackish to freshwater conditions. The small horseshoe crabs may have been partly amphibious, the myriapod probably inhabiting the swamps. The fossils indicate, as shown by Solle and others, that the shales were deposited in quiet, more or less stagnant waters in a lagoon or channel flanked by "mangroves" of psilophytes. The environment and general conditions evidently offered the very best conditions for an invasion of land by the arthropods. The adaptive problems in connection with an occasional or more permanent invasion of the land are discussed in more detail. A study of the Alken fossils and the comprehensive literature of Recent and fossil arthropods indicates that many ancient forms generally regarded as truly aquatic, might have been able to stay on land for shorter or longer periods. The respiratory problems were solved in different ways. Vital to a permanent adaptation to terrestrial life seems to have been the development of a preoral cavity.

The author's address: Prof. Dr. Leif Størmer, Institutt for Geologi, Universitetet i Oslo, Postboks 1047, Oslo 3; Norway.

Kurzfassung.

In vorliegender Veröffentlichung wird der Myriapode *Eoarthropleura devonica* n. g., n. sp., dargestellt. Er gehört in die neue Familie Eoarthropleuridae. Die Art, von der Kopf, letzte Rumpf-Segmente, Ventral-Platten sowie Extremitäten-Reste überliefert sind, ist offenbar mit der karbonischen *Arthropleura* verwandt. — Weiterhin werden folgende Arthropoden-Reste beschrieben: die vermutlich mit einer karbonischen Art verwandte Spinne *Archaeometa ? devonica* n. sp., der Eurypteride *Jaekelopterus rhenaniae* sowie einige bereits früher dargestellte Arten, zu denen neue Einzelheiten gegeben werden. Wenigstens die Mehrzahl der überlieferten Eurypteriden sind vermutlich Exuvien. Einige Funde zeigen eine charakteristische Krümmung, die durch Wasserströmung verursacht worden sein dürfte. — — Die bunt zusammengesetzte Flora und Fauna der Nellenköpfchen-Formation (spätes Unter-Emsium) ist von beträchtlichem paläobiologischem Interesse. Die Pflanzen zeigen ein Wasser- und Sumpf-Milieu an. Gewisse Muscheln waren marin, vertrugen vermutlich aber auch Brackwasser. Der dargestellte Skorpion dürfte im Wasser gelebt haben. Die kleinen Spinnen waren offenbar terrestrisch. Die zur Hughmilleriidae-Stylonuridae-Gesellschaft gehörenden Eurypteriden verweisen auf Brackwasser bis Süßwasser. Die kleinen Limuliden mögen teilweise amphibisch gewesen sein. Die Myriapoden bewohnten vermutlich Sumpf-Gebiete. Die Fossil-Funde sprechen dafür — wie Solle und andere Bearbeiter gezeigt haben —, daß die Tonschiefer der Nellenköpfchen-Formation im stillen, mehr oder weniger stehenden Wasser einer von Psilophyten-„Mangroven" begleiteten Lagune oder Rinne abgelagert wurden. Diese Umwelt und die allgemeinen Bedingungen boten offenbar allerbeste Voraussetzungen für eine Invasion der Überwassergebiete durch die Arthropoden. Die mit einer gelegentlichen oder länger andauernden Invasion des Landes zusammenhängenden Anpassungs-Probleme werden ausführlicher erörtert. Das Studium der Alkener Fossilien und der umfangreichen Literatur über rezente und fossile Arthropoden deutet darauf hin, daß viele altertümliche Organismen, die im allgemeinen für echte Wasser-Bewohner gehalten werden, zu kürzerem oder längerem Aufenthalt auf dem Lande fähig gewesen sein mögen. Die Atmungs-Probleme wurden auf verschiedenen Wegen gelöst. Die Ausbildung einer Präoral-Höhle scheint für die Dauer-Anpassung an die Existenz auf dem Lande lebenswichtig gewesen zu sein.

Contents.

Introduction 89
Acknowledgments 90
Description of fossils 90
Superclass Myriapoda 90
Class Arthropleurida Waterlot 1934 90
Order Arthropleurida Waterlot 1934 90
Family Eoarthropleuridae n. fam. 90
Eoarthropleura n. g. 91
Eoarthropleura devonica n. sp. 91
Additional fossil remains 113
Class Arachnida Lamarck 1801 114
Order Scorpionida Latreille 1817 114
Scorpionidorum g. et sp. indet. 114
Order Araneida Clerck 1757 115
Superfamily Archaeometoidea Petrunkevitch 1955 115

Family Archaeometidae Petrunkevitch 1949 115
Archaeometa Pocock 1911 115
Archaeometa ? devonica n. sp. 115
Subclass Eurypterida Burmeister 1843 116
Order Eurypterida Burmeister 1843 116
Superfamily Drepanopteroidea Kjellesvig-Waering 1966 116
Family Drepanopteridae Kjellesvig-Waering 1966 116
Alkenopterus Størmer 1974 116
? *Alkenopterus brevitelson* Størmer 1974 117
Superfamily Hughmillerioidea Kjellesvig-Waering 1951 117
Family Hughmilleriidae Kjellesvig-Waering 1951 117
Parahughmilleria Kjellesvig-Waering 1961 117
Parahughmilleria heftei Størmer 1973 117
Parahughmilleria major Størmer 1973 118
Suborder Pterygotina Caster & Kjellesvig-Waering 1964 119
Superfamily Pterygotoidea Clarke & Ruedemann 1912 119
Family Jaekelopteridae Størmer 1974 119
Jaekelopterus Waterston 1964 119
Jaekelopterus rhenaniae (Jaekel 1914) 119
Merostomatidorum g. et sp. indet. 121
Arthropodorum g. et sp. indet. 121
General remarks on the arthropod fauna 123
Preservation 123
Composition of the arthropod fauna 125
Associated flora and fauna 125
The arthropod fauna 126
Palaeoecology of the Alken arthropods 127
Palaeoecology of the Nellenköpfchen-Schichten of Alken 130
Local stratigraphy and sedimentology 130
Attempted reconstruction of life and environment 131
The problems of arthropods invading the land 133
Adaptations to terrestrial life 134
Structural changes to avoid desiccation of body 135
Modifications of existing and development of new respiratory systems 135
Modification of morphological characters related to movement 152
Modification of sensory organs 153
Development of preoral cavity 154
Function of preoral cavity 156
Literature 159

Introduction.

The fifth and last part[1]) of the study of the Alken arthropods comprises primarily a description of the interesting myriapod *Eoarthropleura devonica* which together with terrestrial arachnids links the early Devonian fauna to those of the Upper Carboniferous.

Since the present studies started, the late Mr. Josef Hefter has steadily furnished me with new material collected by him in the quarry of the Alkener Bach-Tal. Certain additional material, including a new spider, is described in the present part.

[1]) Addendum: In Part 4 (Størmer 1974: 373) I have forgotten to include the genus *Syntomopterus* (Kjellesvig-Waering 1969b) in the family Stylonuridae.

Sedimentological and stratigraphical research as well as descriptions of fossil plants and non-arthropod animals provide a comprehensive information on the life and environment during deposition of the Nellenköpfchen-Schichten of Alken. The Lower Devonian landscape, with the partly aquatic and partly terrestrial plants, evidently offered unique opportunities for aquatic animals to adapt themselves to terrestrial life. The arthropod fauna contains transitions from typical aquatic to typical terrestrial forms.

Many trials and errors were made by ancient arthropods in their attempts to conquer the land and many different adaptations were evolved. To help our understanding of these attempts the adaptations, particularly as they are seen in Recent taxa, are described in more detail in the present part.

Acknowledgments.

Primarily I am greatly indebted to the late Mr. Josef Hefter (Koblenz) for permitting me to describe his valuable arthropod-collection from Alken.

Furthermore, thanks are due to Dr. W. Struve (Frankfurt am Main) who has helped in preparing the manuscript and has again provided the German translation of the abstract. Dr. Ch. Waterston (Edinburgh) has very kindly read the manuscript and corrected my English. Valuable advice and help have been rendered by Mr. E. N. Kjellesvig-Waering (Florida), Dr. W. D. I. Rolfe and Dr. J. K. Ingham (Glasgow), Dr. H. Levi (Cambridge Mass.), Dr. M. Claridge (Cardiff), Dr. D. M. Holdich (Nottingham), Dr. D. E. Bliss (New York), Dr. E. B. Edny (Los Angeles), Dr. B. B. Rodendorf (Moscow), Dr. M. F. Glaessner (Adelaide). Furthermore, I wish to thank Dr. K. Bjørlykke, Cand. real. J. Nagy, Mr. H. Chr. Seip and Ph. D. B. Thusu (Oslo). Valuable technical assistance has been rendered by Mrs. Kari R. Öztürk and Mr. O. Brynildsrud for making the drawings and photographs.

Description of fossils.

Superclass Myriapoda.

Class Arthropleurida Waterlot 1934.

Order Arthropleurida Waterlot 1934.

Family **Eoarthropleuridae** n. fam.

Type genus: *Eoarthropleura* n. g.

Diagnosis: Dorsal surface of exoskeleton smooth. Head short. Tergites of some somites with anterior and lateral rims; posterior doublure of axis with longitudinal furrows on dorsal surface. Sternites subquadratic. Limbs with relatively long joints, laterally extended ventral portion of coxa, coxa with endite; no rosette plate present.

Taxonomic relations: As discussed below, the new family is related to the family Arthropleurida Waterlot 1934.

Stratigraphic occurrence: Lower Devonian.

Eoarthropleura n. g.

Type species: *Eoarthropleura devonica* n. g., n. sp.

Derivation of name: Composed of ἕως (Greek) = dawn, and the name of the similar genus *Arthropleura*.

Diagnosis: The same as for the family.

Eoarthropleura devonica n. sp.

Pls. 1-4; text-figs. 1-4, 6-24, 39-41.

Derivation of name: Named after the occurrence of the species in the Devonian.

Holotype: The specimen figured on pl. 1 fig. 1 and text-figs. 6-7, SMF VIII 282, Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main. — Type horizon: Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten. — Type locality: Quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.

Paratypes: All material topo- and stratitypic. — Figured specimens: SMF VIII 246 (pl. 3 fig. 1; text-fig. 12), SMF VIII 248 (pl. 3 fig. 3), SMF VIII 263 (pl. 1 fig. 3), SMF VIII 285 (pl. 2 fig. 5), SMF VIII 286 (pl. 2 fig. 9), SMF VIII 287a (pl. 2 fig. 8; text-fig. 19), SMF VIII 290 (pl. 4 fig. 1; text-fig. 13), SMF VIII 300a, b (pl. 4 figs. 2, 5, pl. 8 fig. 2; text-figs. 13, 15, 18, 21), SMF VIII 302 (pl. 1 fig. 2), SMF VIII 303 (pl. 4 fig. 3; text-fig. 21), SMF 30037 (pl. 2 fig. 4), SMF 30038 (pl. 2 fig. 1; text-figs. 9, 22), SMF 30039 (pl. 2 fig. 6), SMF 30043 (pl. 3 fig. 2; text-fig. 11), SMF 30044 (pl. 2 fig. 2), SMF 30045a, b (pl. 2 fig. 3, pl. 4 fig. 4). — Not figured specimens: SMF VIII 257, VIII 283, VIII 298, VIII 299b, SMF 30042.

Diagnosis: Until more species will be known, the same as for the genus and family.

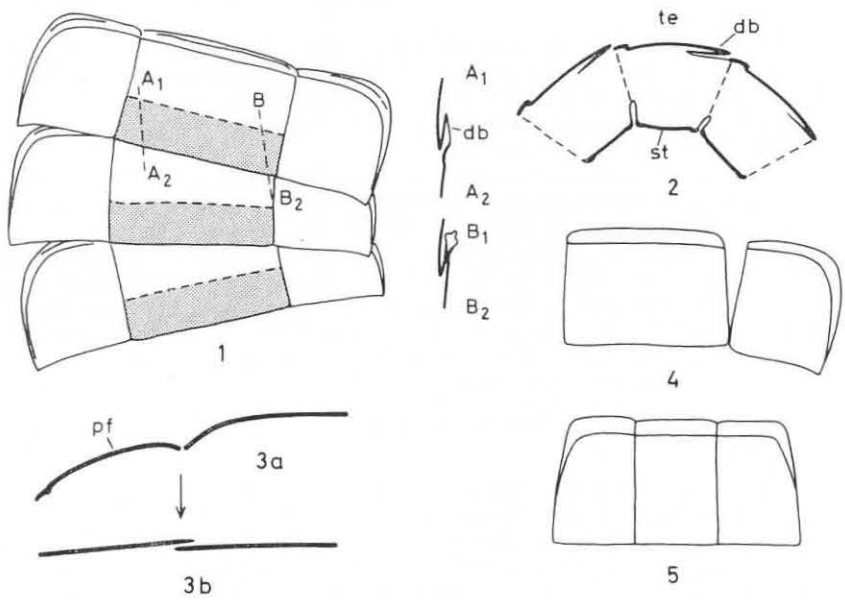
Material: Numerous fragments, particularly of the axis and paratergal folds, have been collected. In isolated cases successive segments are preserved in association (pl. 1 fig. 1a and pl. 3 fig. 2a). In the holotype the first tergite is attached to the head. In the other case five segments of the axis are preserved more or less in situ. — In addition to the dorsal exoskeleton, numerous ventral plates and certain fragments of the appendages have been preserved. The occurrence of these plates together as well as their resemblance to ventral plates in the Carboniferous *Arthropleura* strongly indicate that they all belong to *Eoarthropleura* since no other identifiable arthropod occurs together with the fragments. In two cases (pl. 3 figs. 2a-b, text-fig. 11; pl. 4 figs. 2 and 5; pl. 5 figs. 2-3, text-fig. 15), several plates occur together indicating that they belong to a single or possibly to two disintegrating specimens.

Preservation.

The preserved portions of the exoskeleton are flattened in the dark shale. Evidently at an early stage in the embedding of the plates in the sediment pressure had already caused splitting of the tergites along the axial furrows. In the present preservation the separate plates overlap each other at the axial furrows (pl. 1 fig. 1a, pl. 2 fig. 3, pl. 3 fig. 1a), a feature which suggests that the plates slid over each other as indicated in text-fig. 3b. The original convexity is difficult to determine with certainty, but may have been about as indicated in text-fig. 3a.

In the holotype (pl. 1 fig. 1a) I have removed a small part of the paratergal fold in order to expose the underlying right border of the axis. As shown in text-fig. 6 the over-

lapping amounts to 1·5 mm anteriorly. A similar case is demonstrated in a presumed penultimate body-segment (pl. 3 fig. 1a, text-fig. 12). Here the left paratergal fold overlaps the axis by about 2·5 mm. The full width of the two segments in the flattened state is shown in text-figs. 6 and 12 respectively. In the reconstructions (text-figs. 8 and 14) the probable original convexity is suggested. The wrinkled surface of some of the specimens (pl. 2 fig. 2) indicates that the exoskeleton at least in certain cases was very thin and had become soft so that it could easily be wrinkled by compression. The skin might have been partly dissolved before or during the embedding (comp. p. 123).



Text-figs. 1-5. Movability and splitting of the trunk tergites. — Not drawn to scale. — db = posterior doublure of axis; pf = paratergal fold; st = sternum; te = tergite.

1-4. *Eoarthropleura devonica* n. g., n. sp. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

1: Horizontal flexibility of the body. A_1—A_2 and B_1—B_2 are longitudinal sections with doublure and intersegmental (arthrodial or conjunctural) membrane.

2: Vertical flexibility of the body.

3: Splitting and sliding over of the dorsal plates. — a) original position. — b) splitting and sliding after compression.

4: Splitting off of paratergal folds along the axis (diagrammatic).

5. *Scolopendra viridicornis* Newport 1836. — Recent.

5: "Längsnähte" in the chilopod tergite provide flexibility to the body. [After Manton (pars) 1965: text-fig. 37.]

General description.

The body.

Since no complete specimen is known, it is not possible to determine the length of the body. In one specimen only, several succeeding body segments are preserved almost in place (pl. 3 fig. 2c; text-fig. 11). The axial tergites are mutually much alike and the frequent occurrence of other tergites of similar shape and size may suggest that the body was fairly long and narrow with a considerable number of somites. As shown in table 1 and text-fig. 10 the length of the paratergal folds (pleurae) is rather constant (from 8·3-11 mm) except in the young specimen SMF 30038 where it is 5·8 mm. In most tergites the axial furrows are parallel, only in the first and last ones do the furrows converge and diverge in the anterior direction respectively. The shape of the body was probably elongate with fairly parallel sides and well rounded anterior and posterior portions as suggested in the reconstruction (text-figs. 45-46).

Table 1. Dimensions in mm of paratergal folds (see text-fig. 10).

No.	length axis	width axis	length paratergal folds	width paratergal folds	ratio l/w paratergal folds
SMF 30038	5·2	4·4 5·3	5·8	4·3	1·372
SMF VIII 283			9·2	6·5	1·292
SMF VIII 283			9·2	6·5	1·415
SMF VIII 282a	10·6	12 16·2	10	8·5	1·176
SMF VIII 299b			10	8·5	1·176
SMF VIII 302			10·1	8·5	1·188
SMF 30042	10·5	11·5	10	7·5	1·333
SMF VIII 282b			10·2	8·5	1·212
SMF VIII 297			11	7·5	1·467
SMF 30037			11	8·1	1·358

The head.

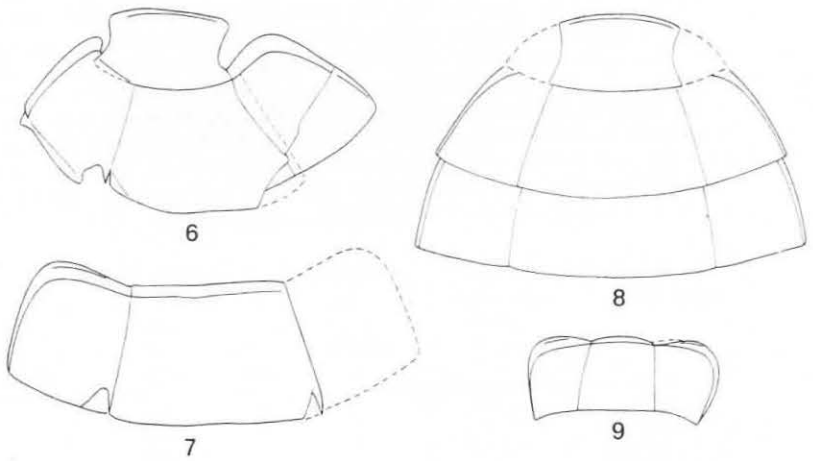
In the holotype (pl. 1 fig. 1; text-fig. 6) the major part of the head shield is preserved. In the present preservation the outline of the portion preserved is subrectangular with convex anterior and posterior margins and with concave lateral margins. Before compression the rear border may have been straighter in dorsal view. The length of the preserved median portion of the head is slightly over one half of the width. A narrow less distinct rim is indicated at the anterior border. The concave lateral borders probably represent "facial sutures" separating the median "cranidium" from free cheeks which have been lost. Lateral eyes may possibly have been present along the sutures. Because of the general outline of the first tergite it seems reasonable to assume that the free cheeks had a convex anterolateral margin as suggested in the reconstructions (text-figs. 8 and 45).

The tergites of the trunk.

The first and second tergites are demonstrated in the holotype (pl. 1 figs. 1a-b), the second tergite lying apart from the holotype on the same piece of shale, but probably belonging to the same individual. The first tergite has a concave anterior and a convex posterior border. This is to minor extent due to compression, but the paratergal folds were evidently directed somewhat forward in life. The smooth median subtrapezoidal axis is separated from the paratergal folds by anteriorly converging axial furrows. The smooth paratergal fold has a trapezoidal outline with the transverse borders forming the

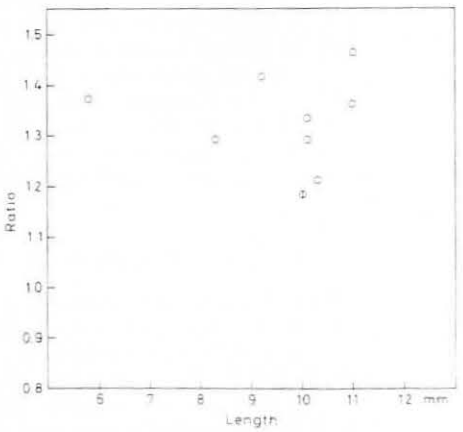
parallel borders. The anterolateral corners are rounded. A flat rim borders the anterior and lateral border of the paratergal fold. It is broadest at the anterolateral corner and decreases in width toward the posterolateral corner where it disappears.

Specimen SMF VIII 300a may also represent the first tergite (text-fig. 13).



Text-figs. 6-9. Head and tergites of the trunk in *Eoarthropleura devonica* n. g., n. sp. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

6. Holotype, representing the head without the free cheeks and eyes (?) as well as the first tergite of the trunk. Stippled line shows the lateral border of the axis below the overlapping paratergal fold (comp. with text-fig. 3). SMF VIII 282a; × 1·8 (see pl. 1 fig. 1a).
7. Probably second tergite of holotype. SMF VIII 282; × 1·7 (see pl. 1 fig. 1b).
8. Reconstruction of the anterior portion of body in dorsal view. About × 2.
9. Paratype, tergite of a small specimen. SMF 30038; × 1·9 (see pl. 2 fig. 1).



Text-fig. 10. Variation in size and shape of the paratergal folds in *Eoarthropleura devonica* n. g., n. sp. The length of the folds in apparently adult specimens is about 9-10 mm. The ratio length width varies from about 1·2 to 1·4. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

The second tergite (pl. 1 fig. 1b; text-fig. 7) has the axis and the left paratergal fold preserved. Diagonal wrinkles on the latter indicate a flattening of the fold. Also in this second tergite the paratergal folds are directed somewhat forward, and the axial furrows converge slightly. The anterior rim of the axis has a vertical posterior margin. A faint transverse furrow is present behind the anterior margins.

The paratergal folds, paranota of HOFFMANN (1969), have a subquadratic outline, the length slightly exceeding the width. The marginal rim forming a continuation of the rim on the axis, is broad anteriorly particularly at the anterolateral corner. A narrow anterior band bordered by a transverse furrow is indicated on the rim.

The typical tergite of the trunk has a rectangular outline with but slightly prolonged posterolateral corners (pl. 2 fig. 3). In a young specimen (pl. 2 fig. 1) the lateral margins are more convex than in the adults. The surface is smooth. In one case (pl. 2 fig. 6) a narrow furrow runs along the posterior margin and on the lateral rim of the tergal fold. It looks like a suture line, but since it is lacking in other specimens it is probably accidental.

Two specimens deviate from the normal ones but this may be due to a different preservation. The plate on pl. 2 fig. 5 could be a tergite the right axial furrow of which is obliterated. In the short tergite on pl. 1 fig. 3 (to the right) the posterior half is broken off, possibly above the anterior border of the doublure.

The doublure:

In several specimens the posterior ⅔ of the axis have the impression of numerous longitudinal furrows (pl. 1 fig. 3, pl. 2 fig. 3, pl. 3 figs. 2a and 3; text-fig. 11). Details are demonstrated in SMF 30043 (pl. 3 fig. 2a). The striated surface occurs at a level just below the dorsal exoskeleton of the tergites, and the striae occur on the dorsal surface of an underlying plate which is smooth on the ventral side. The striated lower plate evidently represents the posterior doublure of the axial tergite. Similar structures are not found on the paratergal folds. An intersegmental or arthrodial membrane evidently connected the anterior margin of the doublure with the anterior margin of the succeeding tergite (text-figs. 1-2).

Because of the long axial doublure the body evidently possessed an unusual flexibility both in the horizontal and vertical plane. By making horizontal turns the paratergal folds would slide over each other as suggested in text-fig. 1. The intersegmental membrane would be streched on one side and curled up on the other. Text-fig. 2 illustrates the inflection of the body in a vertical plane. Each tergite slides over the one behind and the soft integument on the dorsal side is but little exposed. When the trunk was flexed in the vertical plane the sternites on he ventral side were packed together (and might possibly have been pushed under each other as discussed below). Great mobility is found among Recent myriapods not in the least among the primitive Symphyla. The flexibility is obtained in certain groups by the presence of extra short tergites between the longer ones (heteronomy).

Longitudinal sutures of the trunk:

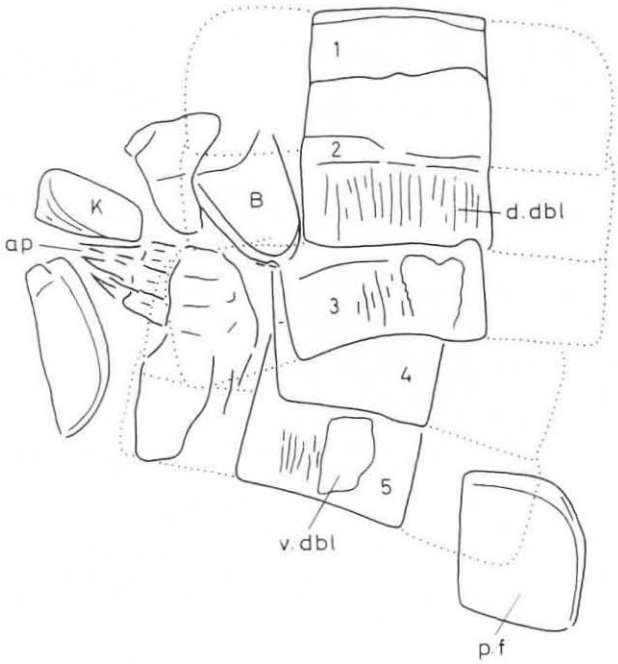
As mentioned above the tergites tend to break along the axial furrows. Open ruptures and overlapping of the plates are visible in many specimens (pl. 1 figs. 1a-b, pl. 2 figs. 1, 3 and 6, pl. 3 fig. 1a). In a young specimen (pl. 2 fig. 1) only the anterior portion of the skeleton is broken along the axial furrows. A further indication of lines of rupture along the axial furrows is the common occurrence of single pieces of the axis and paratergal folds.

Are these lines real sutures or only lines of rupture due to flattening of convex structures? In *Arthropleura*, which evidently is related to the present form, this question has been discussed at length (ROLFE 1969: *R* 628). Most authors have been inclined to regard them as true sutures forming hinge lines along which the paratergal folds could

be moved up and down in relation to the axis. ROLFE, however, suggests that they represent lines of rupture due to flattening of convex structures.

Studies on Recent myriapods are of importance in this connection. In the Chilopoda the dorsal and ventral sclerites have longitudinal "Längsnähte" which divide them into three parts (MANTON 1965: 265) and, thus, correspond in position to the axial furrows in *Eoarthropleura*. The lines (text-fig. 5) represent a break in the endocuticle or a reduction of its thickness. The sutures, thus, form hinge lines along which the tergal folds might be moved up and down offering additional flexibility to the body. Pl. 8 figs. 4-5 indicate the "hinge lines" in a large Recent centipede.

A comparison with Recent Scolopendriomorpha seems to indicate that *both Eoarthropleura and Arthropleura possessed longitudinal sutures serving as hinge lines for the paratergal folds, and which opened during moulting.* In Amphipoda the anterior tergites split along the "axial" furrow during moulting (HENRIKSEN 1932).

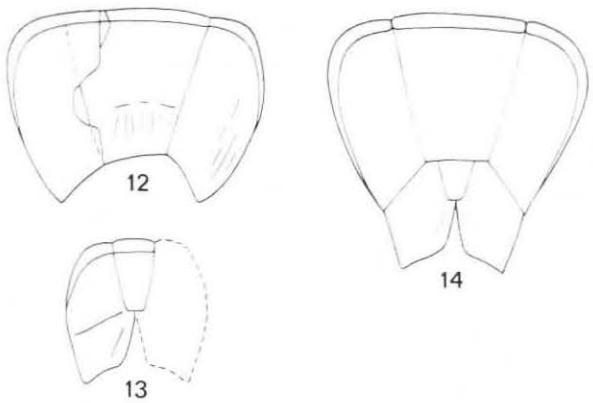


Text-fig. 11. *Eoarthropleura devonica* n. g., n. sp. — Paratype; SMF 30043; × 2·1 (see pl. 3 figs. 2a-b). Specimen showing five succeeding axial tergites, a paratergal fold and remains of ventral plates and appendages. Only one paratergal fold is preserved (down to the right). Stippled lines indicate the outlines of the lost paratergal folds along the axis. The prominent posterior doublures of the axis are striated on the dorsal surface and smooth on the ventral. The fragments of the B and K plates as well as the appendages are indicated. — ap = appendage; B = B plate, a coxal extension; d.dbl. = dorsal surface of doublure; K = K plate or endite; p.f. = paratergal fold; v. dbl = ventral surface of doublure. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

The tail.

Two tergites (pl. 3 fig. 1a, pl. 4 fig. 1; text-figs. 12-14) probably represent the two last major somites. (It is not possible to decide whether one extra quite small somite was present or not.) The former probably represents the penultimate segment. A further cleaning of the specimens has shown that the paratergal fold on the left side has slid over the axis as mentioned above. The axis has a subtrapezoidal outline with the transverse rear margin only about half the length of the margin in front. The length of the axis is about equal to the length of most tergites of the trunk. The paratergal folds are oriented in a posterolateral direction resulting in a concave posterior and convex anterior and lateral margin of the tergite. The tergite has an anterior rim which has its largest width at the anterolateral corners, and decreases in width backwards.

The presumed terminal tergite (pl. 4 fig. 1; text-fig. 3) has a very narrow axis at the posterior with a well marked anterior rim. The posterior width of the axis is about half the anterior width and only about one fourth the length of the axis. The paratergal fold, preserved only on the left side, has a considerable posterior and median extension behind the axis which leaves only a small space to accommodate a possible telson between the rear portions of the paratergal folds. A faint furrow crossing the left paratergal fold from the lateral margin to the end of the axis may be accidental. The inner band of the posterior portion of the tergal fold may have been kept horizontal during life whereas the main portion was laterally inclined.



Text-figs. 12-14. Tail segments of *Eoarthropleura devonica* n. g., n. sp. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

12. Paratype, probably penultimate segment with posterior doublure of axis indicated; the left paratergal fold has slid over the axis, whereas the right fold has been laterally compressed as suggested by the wrinkles; SMF VIII 246a; × 1·9 (see pl. 3 fig. 3).
13. Paratype, probably ultimate segment; SMF VIII 290; × 2·0 (see pl. 4 fig. 1).
14. Reconstruction of the two tail segments; because of the prominent doublure the penultimate tergite covered a considerable portion of the posterior segment; not drawn to scale.

Ventral plates and appendages.

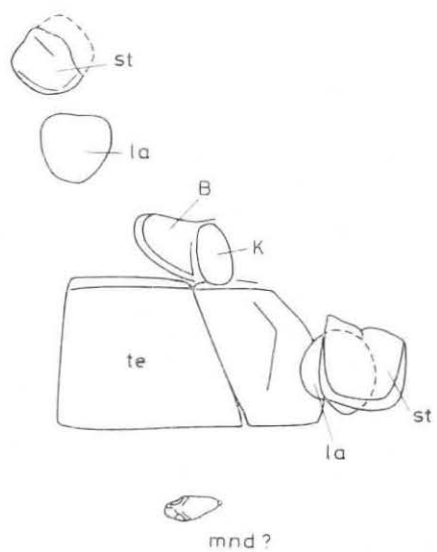
Several different plates occur together with the tergites of *Eoarthropleura*. In certain cases different plates occur together close to tergites. This is the case in the specimens SMF VIII 300 (text-fig. 15) and SMF 30043 (text-fig. 11). Also because we know the other arthropods in the Nellenköpfchen Shale it can hardly be doubted that the fragments described below do belong to *Eoarthropleura devonica* n. g., n. sp.

The plates which are of different shape, might be divided into symmetric (bilateral) and asymmetric plates. The former evidently had a median position on the ventral surface, whereas the latter were laterally located, forming parts of the appendages.

Symmetric plates.

The cordate plates: Two specimens of this plate have been found, both in connection with the tergite in SMF VIII 300 (pl. 2 fig. 7, pl. 4 fig. 2, pl. 8 figs. 2a-b; text-figs. 15-17). One plate (pl. 2 fig. 7) occurs separately, the other (pl. 4 fig. 2, pl. 8 fig. 2) was discovered underneath a subquadratic plate (sternite) which was removed in order to expose the striated plate below. Both cordate plates agree in size and shape; the former measures 4·1 mm in length and 5·0 mm in width; the latter, which is somewhat distorted, measures 4·0 mm in length and 5·0 mm in width. The outline is cordate with a shallow anterior concavity, otherwise well rounded. A moderate convexity is largely maintained. The plate seems to have been solid. Distinct transverse terrassic lines with an anterior convexity occur on the surface. In one of the specimens (pl. 8 fig. 2) the lines alternate somewhat on the left and right side; they do not always meet along the median line.

The subquadratic plates: Several specimens of this type have been found (pl. 2 figs. 8-9, pl. 3 figs. 1b and 3, pl. 4 fig. 2; text-figs. 15 and 18-20). In general the anterior border is not well preserved, probably due to the test being thinner in that region. However, in specimen SMF VIII 246b (pl. 3 fig. 1b; text-fig. 14) the anterior portion is distinctly bilobed with a deep median notch. This plate evidently belongs



Text-fig. 15. *Eoarthropleura devonica* n. g., n. sp. — The positions of the ventral plates in relation to the anterior tergite. Combined from the paratype SMF VIII 300a and its counterpart 300b; × 2·1 (see pl. 4 figs. 2, 5, pl. 8 figs. 1-2). One of the cordate plates was to a great extent covered by one of the sternites (see pl. 4 fig. 2, pl. 8 fig. 2). — B = B-plate, a coxal extension; K = K-plate or endite; la = cordate plate or labrum (?); mnd ? = mandible (?); pt = paratergal fold; st = sternite; te = tergite. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

to the penultimate somite. A median anterior notch is suggested also in two other specimens figured (SMF VIII 287a, pl. 2 fig. 8; SMF VIII 300a, pl. 4 fig. 2); a fifth specimen (SMF VIII 286, pl. 2 fig. 9) is imperfectly preserved in front. The outline of the plate is subquadratic in SMF VIII 246. Characteristic of the plates is their well developed posterior rim which continues forward along the sides, diminishing in width as it is traced anteriorly disappearing halfway towards the front. The central portion of the plate is slightly convex with a smooth surface. One specimen (SMF VIII 248, pl. 3 fig. 3) has a straight anterior border with an isolated tergal doublure in front. It is somewhat doubtful, however, whether or not this plate belongs to the subquadratic plates.

Asymmetric plates.

There are three kinds of asymmetric plates of which two usually occur together. Since they resemble and probably are homologous with two ventral plates in *Arthropleura*, they are here called the B- and K-plates. These plates have a nearly constant shape and size and cannot be confused with posterior tergites.

The B-plate (pl. 4 figs. 3a-b, 4 and 5; text-figs. 11, 21 and 22): This plate has an elongate subtriangular outline; the median straight border abuts to the K-plate. The B-plate forms an elongate rather flat lobe with a rounded distal margin. A broad lateral rim extends as far as to the transverse posterior border. The lobe was probably moderately convex before it became flattened in the shale.

The K-plate (pl. 4 figs. 3a-b and 5; text-figs. 11, 21 and 22): This elongate longitudinal plate abuts to the B-plate along a fairly straight margin. In SMF VIII 303 (pl. 4 figs. 3a-b) the two plates are slightly separated suggesting that the dividing line is a suture, perhaps serving as a hinge line. The anterior, lateral and posterior borders are moderately convex. The width of the subrectangular plate is half the length. Concentric striae or "terrace lines" are present on the lateral and anterior portions of the plate. They enclose parts of a central smooth area which extends to the posterior and median border. The course of the striae shows that the plate is asymmetric. The length of the K-plate is 6·6 mm in SMF VIII 303b, 4·5 mm in SMF VIII 300b and SMF 30045. Since the average tergite length is about 10 mm, the K-plates would be about half the total length of the trunk tergites.

The small elongate plate (pl. 8 fig. 1; text-figs. 15 and 23a-b): This plate occurs together with other ventral plates in specimen SMF VIII 300a (text-fig. 15). It is very probable that it also belongs to *Eoarthropleura devonica*. The solid plate has an ovate outline with a more narrow extension provided with a small terminal knob. The surface has several ridges radiating from a more central point in the broader portion of the plate.

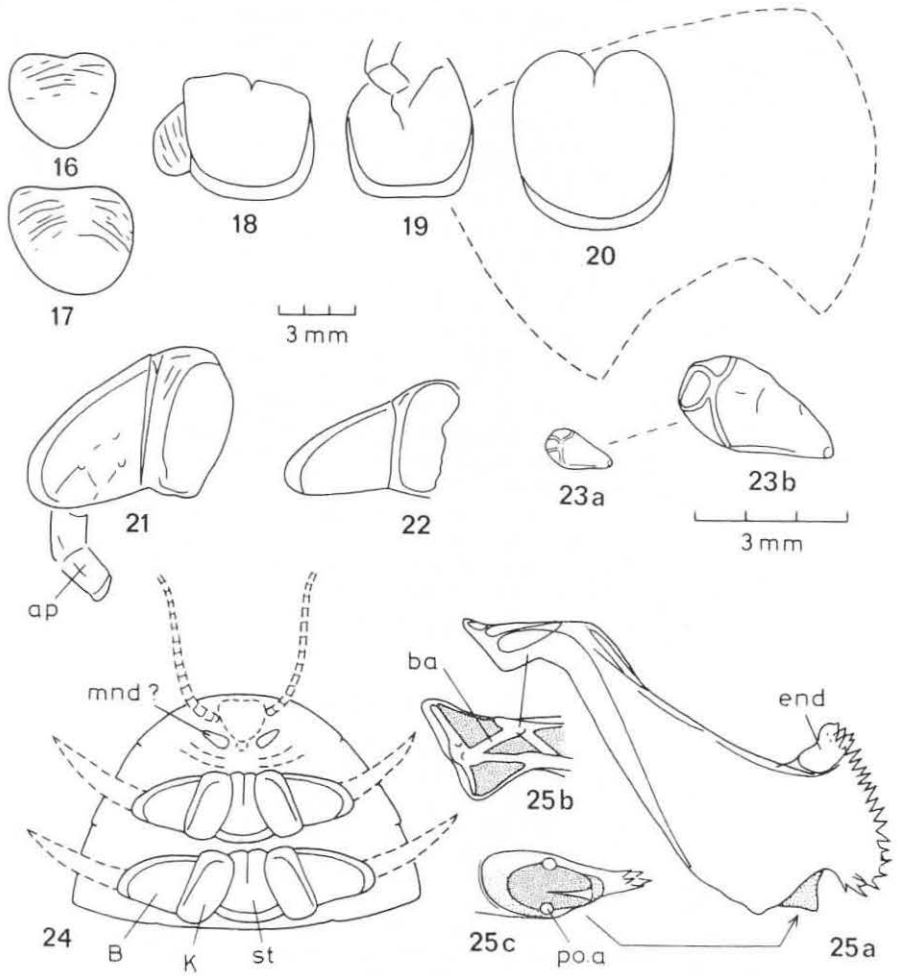
Appendages (pl. 3 figs. 2a-b, pl. 4 figs. 3a-b; text-figs. 11 and 12).

We do not know whether or not antennae were present, but since this is very likely from a comparison with the Myriapoda this is indicated in the reconstruction (text-figs. 45-46). — The legs of the trunk are little known. Proximal joints are demonstrated in the specimen on pl. 4 figs. 3a-b and text-fig. 21 which represents an imprint of the B- and K-plates and the appendage. The leg has a dorsal position in relation to the B-plate which means that the plate covered the base of the appendage in ventral view. The leg-joints are rectangular to subquadratic in outline, the length slightly exceeding the width. Four joints are suggested in the curved leg. At the posterior border of the joints one or two knobs are faintly indicated. — In the specimen with five axial segments (pl. 3 figs. 2a-b; text-fig. 11) the tips of several appendages are indicated. The preservation is not good enough to show any details, at least in a photo-

graph. However, certain spines seem to have been present on the distal joints. If the present position of the legs in relation to the axis was the original one, the tips of the legs would project beyond the margins of the paratergal folds as suggested in the reconstructions (text-figs. 40-41, 45 and 46).

Interpretation of morphological structures. A comparison with *Arthropleura* and Recent Myriapoda.

For more than a hundred years remains of the gigantic myriapod *Arthropleura* have been known from the Upper Carboniferous of the Euramerican floral belt. This unique form appears suddenly in these late Palaeozoic beds and no predecessors were



previously known. The present find of the related *Eoarthropleura* in the Lower Devonian, some 60-70 million years earlier, is therefore of particular interest.

The genus *Arthropleura* JORDAN in JORDAN & MEYER 1854 has been studied by many authors and has recently been dealt with by ROLFE & INGHAM (1967) and by ROLFE (1969) in the Treatise, where a more complete list of the literature is recorded. The morphology of the genus is fairly well known except for the head, tail and base of appendages. As shown below, the new genus *Eoarthropleura* has several major characters in common with *Arthropleura*. The presence or absence of important characters in one or other of the genera may help in our understanding of these structures in both genera.

Thanks to Dr. ROLFE at the Department of Geology of the Hunterian Museum, Glasgow, the University of Oslo has received casts of several specimens of *Arthropleura armata* JORDAN & MEYER 1854. Most specimens are isolated appendages with the characteristic and much discussed rosette plate. Of particular interest is a cast of a

---

◄

Text-figs. 16-25. Ventral structures in *Eoarthropleura* and *Limulus*. — ap = appendage; B = B-plate or coxal extension; ba = skeletal bar serving as apodeme; end = endite or epicoxite; K = K-plate or endite; mnd = mandible (?); po.a = posterior articulation point; st = sternite.

16-24. Ventral structures in *Eoarthropleura devonica* n. g., n. sp. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

16-17. Cordate plates possibly representing the labrum. — 16: paratype SMF VIII 300b; × 2·8 (see pl. 2 fig. 7). — 17: paratype SMF VIII 300a; × 3·6 (see pl. 8 fig. 2).

18-20. Plates interpreted as sterna (st); of the three plates the last one belongs to the penultimate segment (?), the outline of which is stippled. — 18: paratype SMF VIII 300a; × 3·2 (see pl. 4 fig. 2). — 19: paratype SMF VIII 287a, counterpart; × 2·8 (see pl. 2 fig. 8, counterpart). — 20: paratype SMF VIII 246; × 2·8 (see pl. 3 fig. 1b).

21-22. The B- and K-plates. — 21: paratype, B- and K-plate, with fragments of an appendage, SMF VIII 303b; × 3 (see pl. 4 figs. 3a-b). — 22: paratype, A- and B-plate, SMF VIII 300b; × 3·2 (see pl. 4 fig. 5).

23. Probably a mandible, the gnathal margin not preserved; paratype SMF VIII 300a (see pl. 8 fig. 1). — a) × 3. — b) × 6·7.

24. Reconstruction of the ventral surface of the anterior portion of the body; about × 2. The antennae are hypothetical but since no traces of them are seen on the dorsal surface of the head they were probably ventral rather than marginal or dorsal as in Recent myriapods. The stippled cordate plate is interpreted as a labrum, and a mouth with an unknown number of gnathal appendages was probably situated at the posterior margin and behind it. The arrangement of other plates is largely based on the conditions in *Arthropleura* as discussed in the text.

25. *Limulus polyphemus* (LINNAEUS 1758). — Coxa of a walking leg. — Recent; vicinity of Woods Hole, Atlantic Coast, Mass., USA.

a) coxa showing the endite or epicoxite; about × 1.

b) skeletal bars serving as muscular apodemes; slightly enlarged.

c) articulation points at the joint between the coxa and the telopod; slightly enlarged.

small specimen which shows all the ventral structures in situ (pl. 8 fig. 3). This specimen from the Saar Region in W. Germany has been figured by WATERLOT (1934: text-fig. 20) and ROLFE (1969: text-fig. 392). Originally thirteen somites of the trunk were preserved. The plates and appendages are flattened in the shale, but the overlapping of the plates is important in determining the mutual positions of the structures.

Before we discuss and try to interpret the ventral structures it might be useful to point out the main common characters in the two genera, as well as those which differ.

Characters common to both genera:

(1) Body elongate, probably with a considerable number of uniform trunk somites.
(2) Tergite of each somite with a broad axis separated from the narrow paratergal folds by longitudinal furrows. Axis and folds have an anterior rim with a shallow transverse furrow near the anterior margin.
(3) Axis of the tergites with a prominent posterior doublure.
(4) Ventral surface showing median circular to subquadratic plates with a posterior rim.
(5) Each somite with one pair of powerful appendages.
(6) B- and K-plates occur at the base of each appendage.

Characters not present in both genera:

(1) Surface of the tergites strongly sculptured in *Arthropleura*; surface smooth in *Eoarthropleura*.
(2) B-plates larger and more extended in *Eoarthropleura*, also having a broad anterior rim.
(3) K-plates of *Eoarthropleura* with concentric striation near the anterior and lateral borders.
(4) Anterolaterally situated rosette plate occuring in *Arthropleura* only.

The head.

This part of the body is practically unknown in *Arthropleura*. In *Eoarthropleura* the head is relatively small and broad. The concave lateral borders probably mark the course of "facial sutures". The free cheeks are unknown but probably had a subtriangular outline with curved anterolateral margin. Lateral eyes may have been present along the facial sutures. The surface of the "cranidium" has no traces of antennal foramina such as in most myriapods. The presence of the antennae in ventral position may be interpreted as a primitive feature.

The ventral surface of the head is not preserved in any specimen, but the cordate plate described above may belong to this part of the body. The plate differs from the sternites of which we know those of the middle somites and the presumed penultimate somite of the trunk. A terminal segment would be too narrow for such a plate. As the head is concerned there are two possibilities: The plate could be either a labrum, a plate just in front and partly below the mouth, or a metastoma just behind the mouth. A labrum of this type occurs primarily in trilobites but also to some extent in other recent forms, i. e. in crustaceans and in the Ricinulei (Arachnida) which have a prominent plate (cuculus) in front of the mouth, the embryology of which is unknown. A meta-

stoma or postoral plate occurs in the eurypterids where it covers part of the median portion of the very large coxae of the last pair of the prosomal legs. In myriapods and insects the maxillae might partly fuse into a ventral plate, a gnathochilarium or functional underlip (SNODGRASS 1952: 228, text-fig. 63B), but in this case it is always possible to see lines of fusion between the components forming the sclerite. (A "mentum", a triangular plate of the gnathochilarium, has a superficial resemblance to the cordate plate.) For these reasons it seems possible that the cordate plate represents a labrum or upper lip. This primitive condition is unknown in any Recent or fossil myriapod. However, the embryological development of the primitive Symphyla of the myriapods might perhaps indicate the presence of a labrum. In early stages of *Hanseniella* (TIEGS 1940: 46-62) the stomodeal opening has a ventral position some distance from the anterior margin (text-figs. 26-30). The stomodeal opening and the premandibular sternum behind it become gradually overgrown by the clypeo-labrum which possibly might be homologized with the presumed labrum in *Eoarthropleura* (text-fig. 28). During the further development a preoral cavity is formed (text-figs. 29-30; comp. p. 155). — The germ band and pupoid of Diplopoda may show a similar overhanging "plate" as figured by DOHLE (1974: text-figs. 1, 7-9).

The small elongate plate (pl. 8 fig. 1; text-figs. 15 and 23a-b) occurring with other fragments of *Eoarthropleura*, might be interpreted as one of the gnathites of the head. Since the mandible is the major biting appendage of the Myriapoda, the small and solid plate might be one of these. The mandible of *Cormocephalus calcaratus* NEWPORT 1844 of the Symphyla (text-fig. 34) shows considerable resemblance to our plate. In both cases a narrow extension has a knob which in the living form marks the posterior articulation point. In the fossil form the broader portion has radiating ribs which possibly might be compared with the borders between sclerites in *Cormocephalus*. A gnathal margin is not preserved in the fossil specimen. It is very possible, however, that the apparent detailed similarities might be a case of converge only.

WATERLOT (1949) describes certain structures which he interprets as gnathites of *Arthropleura*. Dr. ROLFE informs me, however, that he and Dr. INGHAM have studied the specimen and find that the fragment is nothing but a large K-plate.

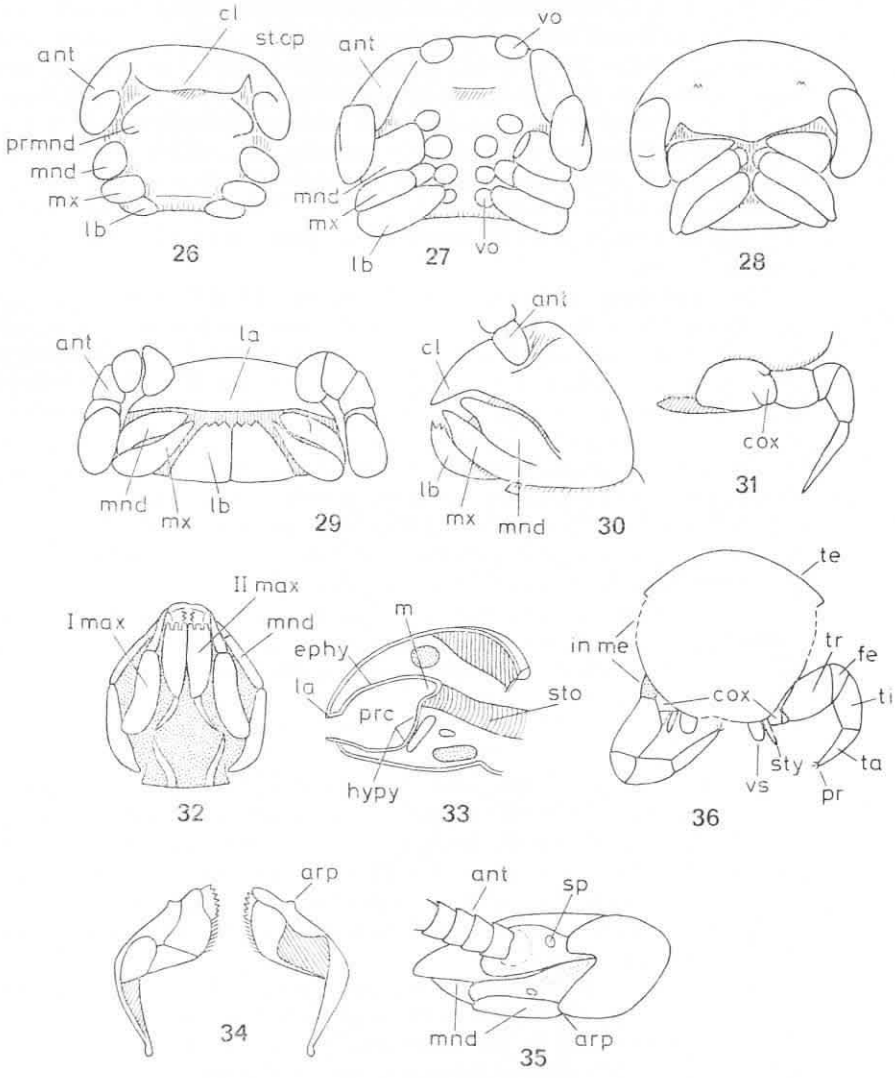
The trunk.

As mentioned above the prevailing occurrence of specimens with parallel axial furrows and the small variations in the relative dimensions of the paratergal folds, suggest that the body of *Eoarthropleura* like *Arthropleura* was elongate with a fairly constant width. The trunk may not have been as long as in *Arthropleura*; a possible length is suggested in the reconstruction (text-figs. 45-46). In the anterior and posterior somites the axial furrows converge towards the front and rear respectively.

The tergites of *Eoarthropleura* resemble in general those of *Arthropleura*. The outlines are practically the same except for a more convex anterior border of the paratergal folds in the latter genus. A distinct difference, however, is found in the surface relief of the tergites of the two genera. In *Eoarthropleura* the surface is quite smooth in contrast to the strongly spinous and tuberculated

surface of *Arthropleura*, a feature, however, which is subject to considerable variation. As mentioned above both genera probably have dorsal longitudinal sutures or hinge lines along the axial furrows. During moulting the tergites probably split along the longitudinal sutures.

The axis of the tergites has a prominent posterior doublure. The structure indicates considerable mobility of the tergites both in the horizontal and vertical plane (text-figs. 1-2). Since the length of the doublure is relatively longer in *Eoarthropleura* than in *Arthropleura* (text-figs. 39 and 42) the flexibility may



have been greater in the former. The dorsal surface of the doublure in *Eoarthropleura* is strengthened by longitudinal ribs and furrows.

The ventral structures of the trunk are demonstrated in situ in several specimens of *Arthropleura* (WATERLOT 1934). Particularly in the smaller specimen from the Saar Region in W. Germany (pl. 8 fig. 3) all the plates and appendages are well preserved in their original position (except for some dorso-ventral compression). In *Eoarthropleura* no plates are found in the original position in relation to the tergites, but their positions may be determined by a comparison with the similar structures in *Arthropleura*.

The median sternites in *Arthropleura* (text-fig. 43) have nearly the same outline and relative size as the presumed sternites in *Eoarthropleura* (text-figs. 18-20 and 40). The main differences are the more narrow posterior rim and the longer and more distinct median furrows in *Arthropleura*. It can hardly be doubted that the presumed sternites in *Eoarthropleura* are homologous with, and situated in the same position as those in *Arthropleura*.

The limbs and their complex of basal plates have also many characters in common in the two genera. In *Eoarthropleura* these structures comprise the limbs and the B- and K-plates, in *Arthropleura* the limbs, the B- and K-plates and the unique rosette plate. In the Devonian species the B- and K-plates often occur together (pl. 4 figs. 3a-b, pl. 4 fig. 5; text-figs. 15, 21 and 22) and are connected in a similar way as in the Carboniferous species. In both cases the two plates are separated by a groove or suture. WATERLOT assumed that the two

---

◀

Text-figs. 26-36. Morphological structures in Recent Symphyla, Chilopoda and Diplopoda. — Not drawn to scale. — ant = antenna; arp = articulation point; cl = clypeus; cox = coxa; ephy = epipharynx; fe = femur; gnl = gnathal lobe; hphy = hypopharynx; in.me = intersegmental membrane; la = labrum; lb = labium; m = mouth; mnd = mandible; I mx, II mx = first and second maxilla; mu = muscle; prc = preoral cavity; prmnd = premandible; pr = pretarsus; sp = spiracle; sto = stomodaeum; st.op = stomodeal opening; sty = stylus; ta = tarsus; te = tergite; tr = trochanter; ti = tibia; vo = ventral organ; vs = ventral sac.

26-31. The symphylan *Hanseniella agilis* TIEGS 1940. (After TIEGS 1940.) Embryological development, showing the gradual formation of the preoral cavity. Text-fig. 31 shows one of the legs after segmentation is completed; the bulbous leg-base includes remains of the ventral organ.

32. The symphylan *Scutigerella immaculata* (NEWPORT 1856). (After SNODGRASS 1952.) Ventral view of the head. The mandibles and maxillae are anteriorly directed and take part in the formation of the preoral chamber.

33. The diplopod *Fontaria virginiensis* GRAY 1832. (After SNODGRASS 1952.) Diagrammatic longitudinal section of the head.

34. The symphylan *Cormocephalus calcaratus* NEWPORT 1844. (After MANTON 1965.) Mandible. Left: ventral view; right: dorsal view.

35. The symphylan *Scutigerella immaculata* (NEWPORT 1856). (After SNODGRASS 1952.) Lateral view of head, showing position of mandible.

36. The symphylan *Scutigerella immaculata* (NEWPORT 1856). (Simplified from MANTON 1966.) Cross section of the body.

plates in *Arthropleura* have a connection only at the anterior border. This is indicated in some of his detailed drawings (WATERLOT 1934: text-figs. 20 and 25), but I have not been able to verify this character, at least not in the well preserved specimen (pl. 8 fig. 3). I agree with ROLFE (1969) that such a "bridge" between the two plates hardly was present.

The K-plate has about the same shape in both genera (text-figs. 40 and 43). The "terrace" lines in *Eoarthropleura* probably serve to strengthen the plate in the same way as in the presumed labrum (pl. 2 fig. 7, pl. 8 figs. 2a-b).

The lobe-shaped B-plate differs in the two genera. In *Eoarthropleura* (text-fig. 39b) it forms a broad lobe covering a major basal portion of the limb. The lobe has a prominent anterolateral rim. In *Arthropleura* (text-fig. 40b) the B-lobe, sensu strictu, is considerably smaller and does not cover the post-coxal portions of the limb but reaches as far as to the ventral basal articulation point of the limb. Characteristic of the B-plate, sensu lato, in the Carboniferous species is the prominent anterolateral lobe called the rosette plate. It forms an extension of the B-plate and must be regarded as part of this plate. In smaller (younger) specimens the rosette plate is of moderate size but develops in larger specimens into a longer, tongue-shaped structure (ROLFE 1969: text-figs. 390-391). In the B-plate of *Arthropleura* the anterolateral rim is more faintly developed than in the B-plate of *Eoarthropleura* but continues on to, and becomes very distinct in the rosette plate. The ventral surface of the rosette plate is very characteristic. It shows a number of mainly wedge-shaped ridges or lobes radiating from the ventral articulation point of the limb (less characteristic in the long rosette plates). WATERLOT (1934) points out that one of the wedges, his C-lobe, differs from the others in being more granulated. The granulation, however, differs between specimens; in large forms even the B-plate may be granulated.

Although a rosette plate is not present in the earlier genus it is possible to imagine a derivation of both the rosette- and B-plate in *Arthropleura* and the lateral lobe or B-plate in *Eoarthopleura* from a common more generalized form with a moderate lateral extension of the coxa (precoxa or metacoxa of authors). A modest lateral extension in a hypothetical form might have developed into the prominent lobe in *Eoarthropleura*. Another trend of development is apparent in *Arthropleura* where the posterolateral portion of the lateral lobe is little developed. The anterolateral portion on the other hand is strongly prolonged and buttressed forming the rosette plate. It seems important, however, that both the rosette plate and the anterior margin of the B-plate, has a marginal rim comparable with the marginal rim of the large lateral lobe or B-plate in *Eoarthropleura*. While the rosette plate probably was rather rigid (although the distal portion is bent upwards in certain specimens), the K-plate might have been more flexible. As pointed out by WATERLOT (1934) and recently to me by Dr. INGHAM and as mentioned below, the K-plate seems to be more bulbous and softer than the B-plate.

In spite of certain differences the K-plate and the B-plate + rosette plate in Arthropleura are probably homologous with the K- and B-plates in Eoarthropleura.

The studies by WATERLOT (1934), ROLFE & INGHAM (1967), ROLFE (1969) and several other authors have shown that the free limb or telopod probably has

nine joints, making ten if we include the coxa. This is a greater number than in most if not all other arthropod legs. The limbs of *Eoarthropleura* are too fragmentary to offer any valuable comparison with *Arthropleura*. The position of the distal portion of the legs in SMF 30043 (pl. 3 fig. 2a; text-fig. 11) indicates, however, that the legs extended well beyond the lateral margins of the trunk as suggested in the reconstruction (text-figs. 45-46). The leg-joints are longer than those in *Arthropleura* (pl. 4 figs. 3a-b; text-fig. 21), and the distal joints seem also in the genus to have been provided with spines along the distal margins.

Interpretation of the basal limb-structures in *Eoarthropleura* and *Arthropleura*.

The nature of the basal plates and their relations to the body wall have been much discussed, and several different interpretations have been offered (ROLFE 1969). The B-plate has been regarded as the basal segment of the limb, and the K-plate as a possible gill-lamella (Kiemenblätter). VERHOEFF (1926-1932) assumed that ventral or coxal sacs present in Recent myriapods might have served as gills in the giant myriapods of the Carboniferous. WATERLOT (1934) interpreted one of the wedge-shaped ridges or evaginations of the rosette plate as a precoxa connecting the limb with the body wall. However, as pointed out by RICHARDSON (1956: 75) and by ROLFE & INGHAM (1967: 120) such an interpretation cannot be accepted. The presumed precoxa (C-plate) forms part of the solid rosette plate and can hardly have had an individual mobility nor would the small sclerite give room for the powerful muscles leading from the body to the appendage.

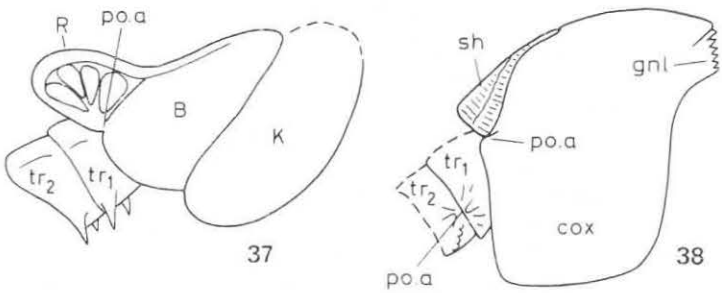
ROLFE & INGHAM (1967) and ROLFE (1969) present another interpretation of the basal structures. Their logical starting point is the assumption that a powerful appendage in a very large arthropod needs a firm attachment to the body wall, and that the body wall between the median sternite and the doublure of the paratergal folds needs to be protected by sclerites such as in Recent myriapods. Accordingly they regard the B- and K-plates including the rosette plate as sclerotized areas of the body wall. The plates are suggested to be "sub-coxal sclerites", comparable with those present in living Chilopoda (comp. MANTON 1958a: 514, 1965: 260, and SNODGRASS 1952: text-fig. 61B, C).

The structures in *Eoarthropleura* present new information regarding the nature and mutual relations of the basal plates in *Arthopleura*. One important point is the fact that the proximal portion of the limb in *Eoarthropleura* is located above the B-plate. In this form at least the B-plate could not have been a sclerite incorporated in the body wall.

In interpreting the mutual relations of the ventral plates in *Arthropleura* it is important to study the young specimen with the ventral plates practically intact (pl. 8 fig. 3). As already mentioned the specimen is flattened in the shale which implies that the plates to a certain extent might have slid over each other as in the tergites (text-figs. 3a-b); however, smaller overlappings of the plates would hardly alter the general picture. In the young individual the posterior portion of the sternite tends to overlap the sternite and K-plate behind. The

median portion of the K-plate overlaps the sternite and the B-plate of the following somite. This arrangement of the plates is also indicated in the reconstruction of ROLFE & INGHAM (1967: text-fig. 2) and ROLFE (1969: text-fig. *R* 387). The rosette plate, forming an anterolateral extension of the B-plate, is partly covered by the appendage of the somite in front. This is particularly characteristic of the larger specimen where the rosette plate is long and tongue-shaped.

The massive buttressing of the rosette plate with the corresponding furrows and bars of the dorsomedian side may have served either as apodemes for muscles or merely as a strengthening of the plate. Ribs or bars serving as apodemes for muscles occur in the coxa of *Limulus* at the joint between the coxa and the body wall (text-figs. 25b-c). (Structures in *Limulus* have also been mentioned by WATERLOT (1934) in connection with his C-plate.) However, in the eurypterid *Moselopterus ancylotelson* (text-fig. 38) the anterolateral corner of the large coxa of the last prosomal leg has a special ornamentation which possibly might be analogous with the rosette plate. The corrugated surface occurring at the point of articulation between the coxa and the first trochanter, probably served to strengthen this vulnerable part of the coxa. Radiating ribs at the same point of articulation between the two trochanters very likely served the same purpose. In the first case (*Limulus*) the rosette plate would be in direct contact with the body wall; in the latter case it represents a prolongation of the coxa. Although the distal portion of the rosette plate evidently has a dorsal



Text-figs. 37-38. Comparison of limb-bases in *Arthropleura* and the eurypterid *Moselopterus*, ventral views. — Not drawn to scale. — B = B-plate; cox = coxa; gn.l = gnathal lobe; K = K-plate or endite; po.a = point of articulation; R = rosette plate; tr_1, tr_2 = first and second trochanter.

37. *Arthropleura armata* JORDAN & MEYER 1854. The rosette plate is attached to the B-plate which forms a ventral portion of the coxa. The K-plate is interpreted as an endite. Two joints of the limb, possibly the two trochanters, are indicated. — Upper Carboniferous; Saar Region, W. Germany.

38. *Moselopterus ancylotelson* STORMER 1974. The large coxa of the last prosomal leg has a ribbed lateral extension or "shoulder" probably supporting the joint between the coxa and the first trochanter which also has radiating ridges probably supporting also the articulation point between the two trochanters. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

position close to the body wall, the fact that it takes part in the articulation and covers parts of the anterolateral base of the appendage (shown also in ROLFE & INGHAM's reconstruction 1967: text-fig. 1) suggests that the rosette plate represents a free extension of the coxa rather than a subcoxal sclerite of the body wall. This view is supported by the structures in *Eoarthropleura* where the lateral extension (B-plate) of the ventral surface of the coxa covers in ventral view the basal points of the appendage.

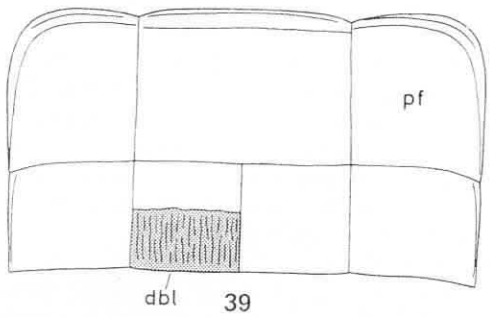
The K-plate which in *Arthropleura* distinctly overlaps the anterolateral portions of the sternum (pl. 8 fig. 3), and in *Eoarthropleura* always occurs connected with the loose B-plate, probably also represents a free median extension of the coxa. The furrow separating the B- and K-plates may to a certain extent represent a hinge line or line of flexibility allowing a limited individual movement of the K-plate.

The K-plate appears as an endite of the coxa. In Recent myriapods (e. g., the Symphyla, text-fig. 32) the gnathal lobe of the mandible is an endite with individual muscles (SNODGRASS 1952). Using the present fossil material it is not possible to decide whether or not the endite of the coxa in myriapods is a primitive structure.

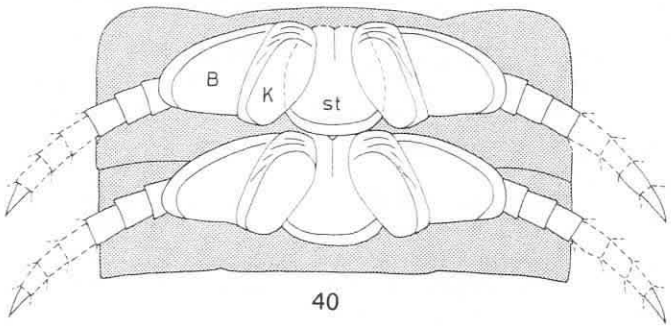
However, if we assume that the K-plate and the rosette plate are true extensions of the coxa, there are no sternal plates, at least not preserved, to which the coxa could articulate and have support. In the Chilopoda the coxa is largely set in a flexible pleuron but there is at least one point of close union with a major trunk sclerite (MANTON 1965: 258). In my opinion, however, it seems possible, that the coxae of *Arthropleura* and *Eoarthropleura* were set in flexible pleuron, without connection with any sclerite. The sclerites forming the long extensions of the coxa, partly cover each other and form together a powerful ventral armour, and at the same time offer strong support to the base of the appendage (pl. 8 fig. 3). If the B- and K-plates were parts of the body wall they probably would have impeded the flexion of the body, particularly in adult specimens of *Arthropleura* where the rosette plate extends far forward.

Dr. ROLFE has recently informed me that he and Dr. INGHAM "now suspect the K-plate to be more than just a plate — it appears to have two surfaces with different ornaments. It may therefore be more in the nature or a flattened sac than a true plate." Dr. ROLFE is very tempted to regard it as an eversible vesicle such as in other Myriapoda, Arachnida, Onychophora etc. As mentioned below I am also inclined to assume that the Arthropleurida had respiratory organs in the form of ventral or coxal sacs. However, I rather doubt that the K-plate represents a flattened vesicle of the kind. A different ornamentation of the dorsal and ventral surface may not be significant. One would except that if the K-plate in *Eoarthropleura* was an eversible sac with a relatively soft and flexible integument, it would hardly have an ornament surface and would rather be expected to be somewhat deformed in some of the occurring specimens. Furthermore, an exposed flexible sac on the ventral side of the body would be easily damaged when the large "centipede" crawled through the plant debris in the swamp.

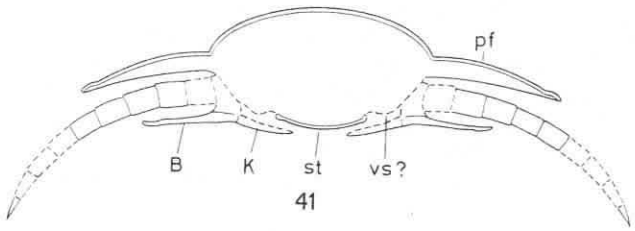
I am more inclined to assume that the K-plate was part of a ventral armour, not merged into the body wall, and that the plate protected an eversible sac on the ventral surface of the body. In the Recent Symphyla a pair of eversible sacs has a median position in relation to the coxae of the same somite (text-fig. 36).



39



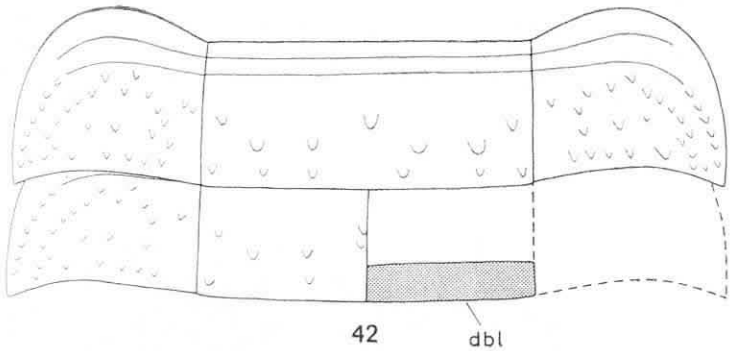
40



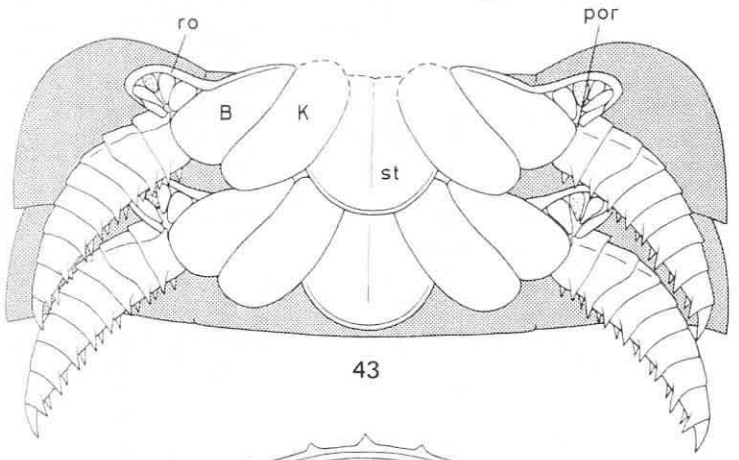
41

Text-figs. 39-41. *Eoarthropleura devonica* n. g., n. sp. Reconstruction of two somites of the trunk. — Not drawn to scale. — B = B-plate or ventral extension of the coxa; dbl = doublure; K = K-plate or endite; pf = paratergal fold; st = sternite; v.s. = ventral sac (?) possibly serving as gill. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

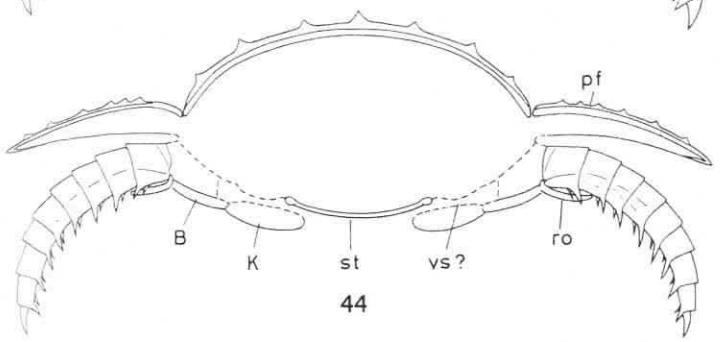
39. Dorsal view with the left half of the second tergite removed to show the dorsal surface of the axial doublure.
40. Ventral view showing the sternites flanked and partly covered by the coxal endites and the extensive lateral extensions of the coxae. (Anterior portion of the second segment erroneously not exposed in text-figs. 40 and 43.)
41. Cross section indicating a possible structure of the coxae and their ventral extensions. The extensive B-plates might have protected some kind of gills which might be homologous and might have had the place of the ventral sacs in primitive myriapods.



42



43



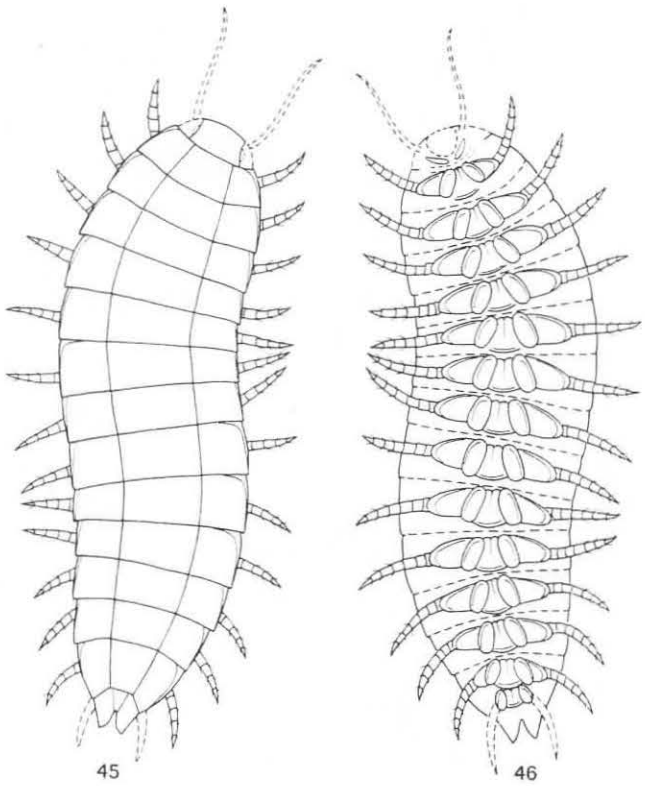
44

Text-figs. 42-44. *Arthropleura armata* JORDAN & MEYER 1854. Reconstruction of two somites of the trunk. — Not drawn to scale. — B = B-plate or ventral extension of the coxa; dbl = doublure; K = K-plate or endite; ro = rosette plate; pf = paratergal fold; por = point of articulation; st = sternite; vs? = ventral sac (?), probably serving as gill. — Upper Carboniferous; Saar Region, W. Germany.

42 Dorsal view with the left half of the second tergite removed to show the dorsal surface of the axial doublure.

43 Ventral view showing the sternites partly covered by the coxal endites (K-plates), and the moderately developed posterolateral extensions (B-plates). The rosette plates form anterolateral extensions of the coxae.

44. Cross section indicating a possible structure of the coxae and their ventral extensions. The K-plates might have protected gills possibly developed from ventral organs or the K-plates are flattened ventral sacs as assumed by ROLFE & INGHAM.



Text-figs. 45-46. *Eoarthropleura devonica* n. g., n. sp. Reconstruction, about × $^{3}/_{4}$. Since the broad doublure indicates a strong horizontal mobility an undulating body is suggested. In the reconstructions the free cheeks, the labrum, antennae and gnathites are hypothetical. The mutual positions of the coxae of the trunk in relation to the sternites are based on structures in *Arthropleura*. The exact number of trunk somites and the presence or absence of tail appendages and a telson are also unknown. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany. — 45. Dorsal view. — 46. Ventral view.

(The embryological development of *Hanseniella* shows that the ventral sac at a certain stage is connected with the coxa forming a bulbous leg-base (text-fig. 31), a feature which to some extent may support the opinion of ROLFE concerning the K-plate being a vesicle attached to the coxa.)

In accordance with Dr. INGHAM's observations the K-plates are given a certain thickness in the reconstruction (text-fig. 44).

Palaeoecology.

In his important discussion on the habitat of *Arthropleura* ROLFE (1969: *R* 614) arrives at the conclusion that the giant "centipede" belonged to the Coal Measure swamps of the Euramerican floral belt (possibly with one exception from the Angaran floran belt), and that it was completely dependent upon this unusual environment. The genus is compared with the Polydesmida of Recent Diplopoda about which MANTON (1954) writes: "These 'flat-backed' millipeds live under dead leaves and loose damp material." "The animals are thus well suited to push into crevices which give way predominantly in one plane, as does the damp layered mass of semidecayed leaves on a woodland floor." This agrees with the studies of WATERLOT (1934: 298) indicating that *Arthropleura* lived near the shore-line and was able, with its presumed gills, to live both in the water and swamps and in among the damp plant debris on land. VAN DER HEIDE (1951: 45) assumes that the arthropleurids were mainly terrestrial, living on the Carboniferous peatbogs.

Eoarthropleura also has the broad and flat head which is characteristic of the Polydesmida among the Myriapoda. *Eoarthropleura* has relatively longer limbs than *Arthropleura*. This and a greater flexibility in the vertical plane indicate that the Devonian form was more agile than the Carboniferous one. It is significant that the associated fauna shows considerable resemblance to that of the Carboniferous swamps (comp. p. 133). It seems very probable that *Eoarthropleura* of the Lower Devonian, like *Arthropleura* of the Upper Carboniferous, lived in tropical swamps or in the "mangrove" swamps along the shores. In the damp and tropical environments gill-like respiratory organs were probably present. It cannot be determined whether tracheae were present or absent.

It is interesting to notice that a gut infilling preserved in a juvenile *Arthropleura* is packed with vegetable debris indicating that these animals were herbivorous or possibly omnivorous (ROLFE 1969: *R* 615).

Taxonomic relations.

Eoarthropleura is evidently related to *Arthropleura*. They both belong to a separate class of Myriapoda. Since the appendages, particularly their basal portions, differ considerably in the two genera, I have found it appropriate to introduce a new family Eoarthropleuridae to include the new genus.

Additional fossil remains.

While I have been studying the specimens collected by Mr. HEFTER from the quarry at Alken, new fossil material has steadily been furnished by this eminent collector. The faunas collected seem to vary from time to time, but this might to a larger extent be due to collecting from single individual blocks of shale rather than from different stratigraphic levels.

In the following pages, additional information is given on taxa which have already been described. One new species, an undetermined scorpion, a previously unrecorded eurypterid and one problematicum are also described.

Class Arachnida Lamarck 1801.

Order Scorpionida Latreille 1817.

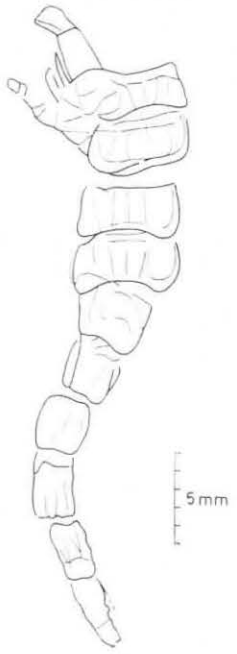
Scorpionidorum g. et sp. indet.
Pl. 5 fig. 1; text-fig. 47.

Material: Mesosomal tergites and part of metasoma, SMF 30047 (pl. 5 fig. 1; text-fig. 47). — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.

Description.

The specimen figured comprises five of the six mesosomal tergites and the main part of the metasoma; furthermore undeterminable fragments of prosomal appendages are present. The prosoma and first tergite as well as the telson are missing, and the last segments of the tail are not well preserved.

The body which may have had a length of about 40 mm, is very narrow. The tergites are subrectangular in outline with concave posterior border and well rounded posterolateral corners. The ratio length width of the segments in the middle of the mesosoma is about 0·46. The tergites have broad marginal rims and distinct longitudinal ridges which also occur on the metasomal segments. The narrow metasomal segments decrease in width backwards. The traces of prosomal appendages which are preserved, probably belong to the pedipalp and walking legs.



Text-fig. 47. Scorpionidorum g. et sp. indet. — Mesosomal tergites, part of metasoma and appendages; SMF 30047; × 2·4 (see pl. 5 fig. 1). — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

Taxonomic relations.

The length of the body is almost twice that of *Waeringoscorpio hefteri* STØRMER 1970 occurring in the same beds (STØRMER 1970). The present species differs also by its more narrow opisthosoma of which the mesosoma is relatively longer than the metasoma in the previously described species. The new species evidently represents another species, but the imperfect preservation does not permit a closer determination.

Order Araneida CLERCK 1757.

Superfamily Archaeometoidea PETRUNKEVICH 1955.

Family **Archaeometidae** PETRUNKEVICH 1949.

Archaeometa POCOCK 1911.

Type species: *Archaeometa nephilina* POCOCK 1911.

Archaeometa ? devonica n. sp.

Pl. 5 fig. 2; text-fig. 48.

Derivation of name: Named after the occurrence of the species in the Devonian.

Holotype: The specimen figured on pl. 5 fig. 2 and text-fig. 48, SMF 30048, Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main. — Type horizon: Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten. — Type locality: Quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.

Diagnosis: Archaeometidae with long narrow opisthosoma without axial furrows, anterior $^{3}/_{5}$ not segmented, posterior $^{2}/_{5}$ divided into four or five segments; surface of opisthosoma smooth.

Description.

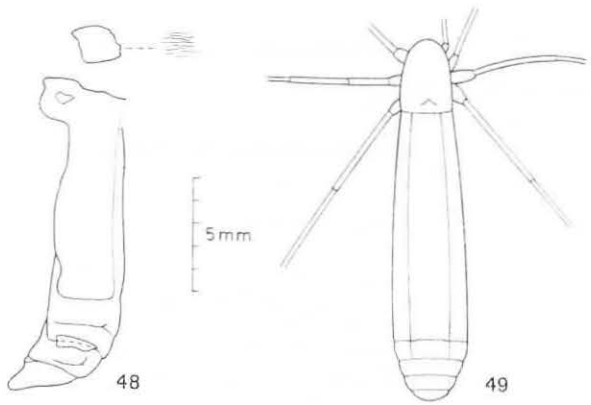
The abdomen (opisthosoma) and probably a smaller portion of the prosoma (?) is preserved. The latter structure is doubtful. Although there is no break between this broader anterior portion and the more narrow portion behind, the former has a minute striation which may suggest that it possibly belongs to a plant rather than a prosoma.

The elongate abdomen measuring 14 mm in length, has a fairly uniform width about $^{1}/_{5}$ the length. It is divided into an anterior unsegmented and a posterior segmented portion, the latter having a length of about $^{2}/_{5}$ of the former. The width of the abdomen increases slightly backwards to the segmented portion and then decreases rapidly to the last blunt part, the latter visible only when emerged in alcohol or some other liquid.

The anterior unsegmented portion has a sloping lateral border on the right side. The posterior segmented portion has four or five segments separated by transverse furrows not reaching the lateral border on the left side. The border between the second and third segment is not well defined because two surfaces, probably the dorsal and ventral surface of the exoskeleton, are exposed at the same time. The blunt and narrow last segment may possibly represent some kind of a telson.

Taxonomic relations.

From the Upper Carboniferous Pocock (1911: 137, text-fig. 11) described a spider which resembles the present species. The specimen which is not well preserved, has more recently been examined by Petrunkevitch (1949: 279, pl. 49, text-fig. 159, pl. 80 fig. 260) who presents a semidiagrammatic reconstruction of the species (text-fig. 49). Both the British and the German species have a strongly elongated abdomen with a relatively short posterior portion composed of four or five segments. The length of the segmented portion is greater in the Devonian than in the Carboniferous species, as predicted by Petrunkevitch (1949: 280). Another difference is the broader terminal portion in *Anthracometa nephilina* Pocock 1911. Because of the differences mentioned and the considerable difference in geologic age a new species is suggested for the Alken specimen.



Text-fig. 48. *Archaeometa ? devonica* n. g., n. sp. — Holotype, opisthosoma with traces of prosoma; SMF 30048; × 3 (see pl. 5 fig. 2). — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

Text-fig. 49. *Archaeometa nephilina* Pocock 1911. — Reconstruction, × 8·2 (after Petrunkevitch 1949). — Upper Carboniferous; Coseley, Staffordshire, England.

Subclass Eurypterida Burmeister 1843.

Order Eurypterida Burmeister 1843.

Superfamily Drepanopteroidea Kjellesvig-Waering 1966.

Family **Drepanopteridae** Kjellesvig-Waering 1966.

Alkenopterus Størmer 1974.

Typus-Art: *Alkenopterus brevitelson* Størmer 1974.

? *Alkenopterus brevitelson* Størmer 1974.

Pl. 5 fig. 4.

Material: A prosoma and mesosoma, SMF VIII 284a, b (pl. 5 fig. 4). — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.

Description.

The specimen figured has been difficult to identify. The protruding first tergite may recall certain Devonian Arachnida. However, a closer study of the specimen and its counterpart indicates that the tergite is dislocated and so occupies a higher position than the rest of the mesosoma. The impression of the metastoma also suggests the eurypterid nature of the specimen. A closer identification is difficult because the dorsal surface of the prosoma and the ventral surface of the mesosoma and the telson are not preserved.

Remarks: Among the eurypterids of Alken only the members of the Drepanopteridae may be compared with the present specimen. The two species of *Moselopterus* are considerably bigger than the eurypterid which is now being considered, but it is not impossible that the latter may be a larval form. *Drepanopterus struvei* Størmer 1974 has about the same size but has a punctate ornamentation which is not present in the new specimen. *Alkenopterus brevitelson* is small and has a smooth surface. Although unfortunately the eyes and telson characteristic of that species are not preserved, it seems probable that the specimen belongs to this species. The ovate metastoma confirms the placing of the genus in the Drepanopteridae.

Superfamily Hughmillerioidea Kjellesvig-Waering 1951.

Family **Hughmilleriidae** Kjellesvig-Waering 1951.

Parahughmilleria Kjellesvig-Waering 1961.

Typus-Art: *Parahughmilleria salteri* Kjellesvig-Waering 1961.

Parahughmilleria hefteri Størmer 1973.

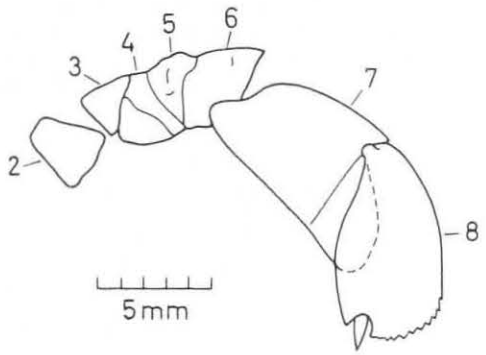
Pl. 6 figs. 1-2.

Material: A coxa of a swimming leg, SMF 30049 (pl. 6 fig. 1) and a small larva probably belonging to *P. hefteri*, SMF 30051 (pl. 6 fig. 1). — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.

Description.

The coxa belonging to the sixth prosomal appendage or swimming leg corresponds to one previously described (Størmer 1973: text-fig. 54), but the basal portion has a more quadratic outline than indicated in the reconstruction (Størmer 1973: text-fig. 84). In the new specimen the gnathal edge is very well preserved. The convex margin has about 17 wedge-shaped, slightly curved teeth. In contrast to the conditions in pterygotids (text-figs. 51b-54b), the anterior teeth are but feebly developed; the most powerful teeth occur in the posterior $^{1}/_{2}$ or $^{2}/_{3}$ of the margin.

The larval specimen (pl. 6 fig. 2) measures 12 mm in length. The prosomal length and width are 2·4 mm and 4·3 mm giving a ratio 0·56. Although the specimen is flattened the ratio conforms with the trend of development indicated in previously measured specimens (STØRMER 1973: text-fig. 37). A relatively larger prosoma with fairly long and broad swimming legs agrees with the conditions in young specimens of *Eurypterus remipes* DEKAY 1825 according to CLARKE & RUEDEMAN (1912: 169) and ANDREWS et al. (1974: 107). Traces of the coxae are seen in the specimen. In the present specimen with a body length of 12 mm the maximum width of the paddle is 0·9 mm corresponding to a ratio of 0·08, against a ration of about 0·064 in the adults.



Text-fig. 50. *Parahughmilleria major* STØRMER 1973. — Swimming leg (VI); SMF 30049; × 3. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

Parahughmilleria major STØRMER 1973.

Pl. 6 fig. 1a; text-fig. 50.

Material: A swimming leg, SMF 30049 (pl. 6 fig. 1a; text-fig. 50). — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.

Remarks:

Because of its large size the specimen figured probably belongs to this species. This is confirmed by the presence of an operculum with a width of 28 mm.

The truncate distal portion of the paddle, resulting in a more subtriangular outline of the palette than the subovate outline in other genera, is characteristic. Previous less complete specimens (STØRMER 1973: 171) have given a number of values for the ratio between various elements of the paddle. The new specimens have the following values, the old averages in parentheses: Ratio length of paddle width of segment 7 = 2·83 (2·72); length of segment 7 width of segment 7 = 1·74 (1·83), length segment 7 length segment 8 = 1·22 (1·22), length segment 7 width segment 8 = 1·84 (1·99), length segment 8 width segment 8 = 1·80 (1·64).

The proximal joints are partly preserved as imprints. It is difficult to identify the different joints but they are evidently less simple than in my reconstructions of *P. hefteri* and *P. major* (STØRMER 1973: text-figs. 84 and 97).

Suborder Pterygotina Caster & Kjellesvig-Waering 1964.

Superfamily Pterygotoidea Clarke & Ruedmann 1912.

Family **Jaekelopteridae** Størmer 1974.

Jaekelopterus Waterston 1964.

Typus-Art: *Pterygotus Rhenaniae* Jaekel 1914.

Jaekelopterus rhenaniae (Jaekel 1914).
Pl. 7; text-fig. 51.

Material: Two coxae of the last prosomal legs (VI), SMF 30053 (pl. 7 fig. 1) and SMF 30054a-b (pl. 7 fig. 3); one metastoma, SMF 30054 (pl. 7 fig. 4); one fragment of a prosoma, SMF 30053a (pl. 7 fig. 2); all finds probably belonging to the same individual. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.

Description.

The prosoma is represented by the very shriveled specimen shown on pl. 7 fig. 2. It is impossible to determine the outline of the shield. An anterior margin is indicated and a large left (?) lateral eye shows a great number of facets. The margin in front (?) has a row of tubercles. The right (?) portion of the plate seems to have been cut off along the apparent longitudinal line.

Coxae of the swimming legs (VI), however, are preserved showing the ventral surface. The outline is not well demonstrated but the gnathal lobe seems relatively prominent in relation to the basal portion. The gnathal lobe has parallel anterior and posterior margins, and a moderately convex median margin. This margin has twelve powerful teeth, the six anterior ones of about equal size, and from then on the size decreases posteriorly, and at the posteromedian angle the teeth are not differentiated. The teeth have a convex anterior and a nearly straight posterior margin. A supporting marginal ridge seems to be present.

The basal portion of the coxa has a distinct ornamented ridge running from the anterior margin of the gnathal lobe obliquely backwards across the basal portion of the coxa. This portion has traces of scales.

A well preserved metastoma has an elliptical outline with a shallow notch in front (text-fig. 51b).

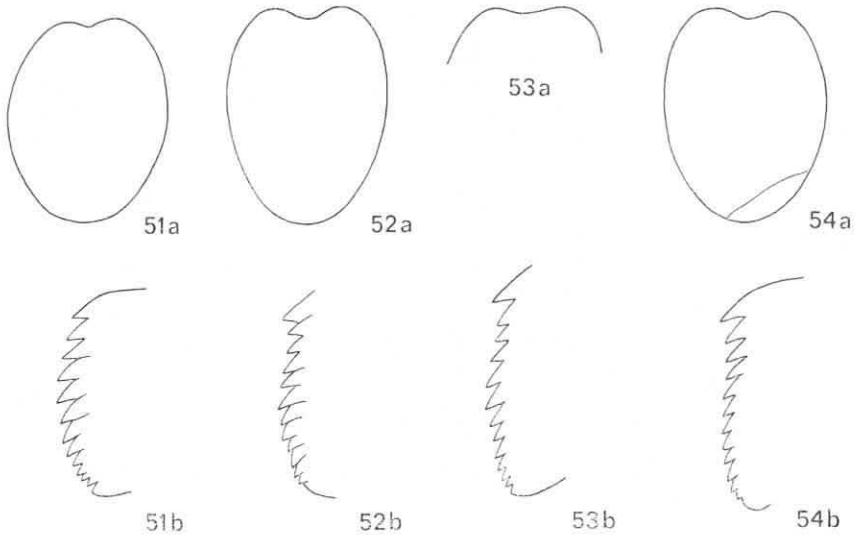
Taxonomic relations.

The taxonomy of the pterygotids has been based chiefly on the characters of the chelicers, the metastoma, the genital appendages and the shape of the telson. Very rarely are all these characters represented in the specimens available. As in scorpions it has become evident that although the dorsal morphological features may be much alike the ventral structures may be very different. For these reasons it is difficult to establish new genera and species. For practical reasons it might be useful, however, to introduce new species based on a few and even on one single character only.

Because of the twelve teeth in the coxa of the swimming foot and an elliptical metastoma with a shallow anterior notch, the present species either

belongs to the genus *Pterygotus* or the genus *Jaekelopterus*. The Lower Devonian *Pterygotus anglicus* AGASSIZ 1844 (text-fig. 54b) has an elliptical metastoma, however, broader in front than in the present species (text-fig. 51b), and the coxa lacks the ornamented crossing ridge. The Lower Devonian *Pterygotus carmani* KJELLESVIG-WAERING 1961 from Ohio (text-figs. 53a-b) has a slightly deeper notch on the metastoma. *Jaekelopterus rhenaniae* (JAEKEL 1914) (text-figs. 53a-b) from slightly older beds of the Rhine area is rather well known (STØRMER 1936), but unfortunately only the frontal portion of a metastoma is preserved. The shallow but broad notch deviates somewhat from the present species. However, the coxae have the same characteristic crossing ornamented ridge. In spite of the difference in the metastoma, the Alken specimen probably belongs to *Jaekelopterus rhenaniae*.

The present remains belong to a relatively small specimen. A very big coxa measuring 27 cm across (STØRMER 1936: text-fig. 7) was evidently derived from an individual which measured 170-180 cm total body length. The present coxa



Text-figs. 51-54. Metastoma (51a-54a) and gnathal margin of coxa of swimming leg (51b-54b) of pterygotids. — Not drawn to scale.

51. *Jaekelopterus rhenaniae* (JAEKEL 1914). — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.
52. *Pterygotus carmani* KJELLESVIG-WAERING 1961. (After KJELLESVIG-WAERING 1961.) — Lower Devonian; Lucas Co., Ohio, USA.
53. *Jaekelopterus rhenaniae* (JAEKEL 1914). (After STØRMER 1936.) — Lower Devonian, Wahnbach-Schichten; Overath E. Köln, W. Germany.
54. *Pterygotus anglicus* AGASSIZ 1844. (After WOODWARD 1866-1878.) — Lower Devonian; Forfarshire, England.

measuring 2·5 cm across would correspond to a specimen with a body length of about 16 cm. Pterygotic scales previously described (STØRMER 1974: pl. 12 fig. 4) show that larger specimens also were present at Alken.

WEIDMANN (1967) has described a prosoma of a pterygotid from the Siegen-Schichten of a quarry about 30 km WNW. of Alken. The prosoma which differs from *J. rhenaniae* by its more subquadratic shape may belong to another species or genus.

Merostomatidorum g. et sp. indet.

Pl. 6 fig. 3.

Material: Two plates, SMF 30050 (pl. 6 fig. 3). — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.

Description.

The two coarsely tuberculated plates might belong to the Merostomata. The outlines are not distinct but a fairly truncated posterior margin is suggested in the left specimen. Otherwise the outline seems rather circular, and concentric ridges indicate that the plates had a considerable convexity in life. The ornamentation consists of scattered elongate pustules, about 0·6-0·7 mm in length with a fine granulated surface in between. The diameter of the plates varies from 11-14 mm.

Affinities.

The species differs by its particular ornamentation from ?Stylonuridarum g. et sp. indet. figured in part 4 (STØRMER 1974: pl. 13 fig. 7). The outline and convexity recall the ventral abdominal shield of the synziphosuran *Diploaspis* (STØRMER 1972), but the ornamentation appears to be different.

Arthropodorum g. et sp. indet.

Pl. 5 fig. 3; text-fig. 55.

Material: A flattened specimen, SMF 30048 (pl. 5 fig. 3; text-fig. 55). — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.

Description.

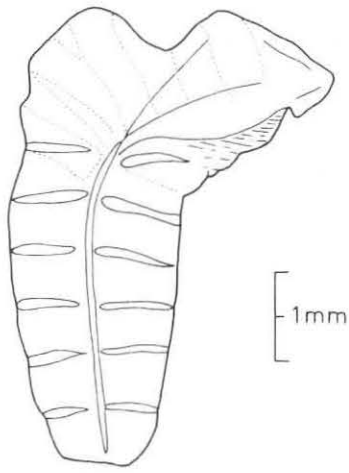
The length of this segmented specimen is about 6 mm, measured along the median axis. The posterior elongate portion is relatively well preserved, whereas the anterior is less distinct and has to be studied immersed in a liquid.

The elongate posterior portion consists of 6 segments bordered by fairly broad transverse grooves. A broad median groove runs forward from the last segment into the anterior portion of the specimen. Here the median groove disappears; only the right wall of the groove remains as a bend in the exoskeleton. Two ridges are actually present but one is evidently accidental. Immersed in alcohol, the anterior portion of the fossil shows a distinct segmentation as indicated in text-fig. 55. The segmented borders appear as faint transverse lines. Posteriorly they cross the coarse transverse grooves. This suggests that the segmentation distinguished by the fine lines might belong

to one surface and the segments marked by the coarse grooves to another. As indicated in the drawing, the anterior triangular portion of the body has no traces of crossing furrows. This part may possibly represent the head of the animal. Behind the presumed head 7 partly dislocated segments are indicated in addition to the posterior segments. To the right a marginal surface shows parallel striae.

Affinities.

The small animal which possibly had a triangular head and probably 13 following segments, can hardly be taxonomically determined. It is not possible to decide whether it was a primitive chelicerate or it belongs to the Myriapoda-Insecta groups. The more or less contemporaneous *Rhyniella praecursor* described by SCOURFIELD (1940) from the Rhynie Chert Beds has been regarded as belonging to the Collembola and thus representing the earliest known insect. SHAROV (1966: 76) assumes that the first insects probably were similar to members of the Lower Permian Order Monura described by him. In these forms "the trunk is homonomously segmented into 14". In the Alken form 13 segments are noticed but an extra terminal one might possibly have been present. SOLLE (1970: 65) mentions that the presence of terrestrial arachnids and a true terrestrial flora may presuppose the presence also of insects serving as nourishment for the arachnids. Perhaps the present arthropod specimen is the first indication of insects on the Hunsrück Island. The probable presence of Lower Devonian insects has been discussed by HUGHES & SMART (1967) and by KEVAN & al. (1975).



Text-fig. 55 Arthropodorum g. et sp. indet. — Segmented body fragment; SMF 30048; × 12 (see pl. 5 fig. 3). Dotted lines indicate outlines of ventral (?) plates. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

General remarks on the arthropod fauna.

Preservation.

As usual in black shales the exoskeletons of arthropods are preserved as imprints only, the imprints often being covered by a silver-like film. The exoskeletons were evidently dissolved before and during the embedding and during the diagenesis of the remains (possibly also at a later stage). We may also have had a selective preservation due to differences in the content of inorganic salts. This is demonstrated in the Devonian Hunsrück Shale and the Silurian Ringerike Sandstone faunas (RICHTER 1931: 339; STØRMER 1935: 274), as well as in the Carboniferous beds containing *Arthropleura* (ROLFE 1969: 615).

The present material demonstrates, at least to some extent, a decomposition of the exoskeleton before embedding in the sediment. A paratergal fold of *Eoarthropleura* (pl. 2 fig. 2) and in particular a prosoma of *Jaekelopterus* (pl. 7 fig. 2a) shows very distinct wrinkles indicating that the test was very thin and flexible before it became covered by sediment. Similar badly shrivelled tests are found in certain fragments of crustacean carapaces in the Carboniferous mud-deposits described by ZANGERL & RICHARDSON (1963: 128). They interpret the preservation of the calcareous-phosphatic carapaces either as due to the presence of freshly moulted individuals in the "soft-shell stage", or to the mineral content having leached from the chitinous framework by stomach acids (when the crustaceans were eaten by sharks). As in *Limulus* the inner part of the procuticula may have contained a certain amount of inorganic salts which might have been dissolved before embedding in the sediment (comp. DALINGWATER 1973: 184). The chitinous parts of the exoskeleton were evidently attacked by bacteria (even under anaerobic conditions) and by humic acids deposited in a peat of a swamp.

The fossil remains largely consist of separate plates, but more or less "complete specimens" also occur. Plant remains and pteraspid shields have been transported before embedding as mentioned by FAHLBUSCH (1960), SOLLE (1970) and SCHAARSCHMIDT (1970). This was evidently the case also of the arthropod remains. Transport by currents of empty moults would be easier than of dead individuals.

Exuviae or dead animals.

CLARKE & RUEDEMANN (1912: 25) mention the probability that the majority of remains found being cast exuviae. When *Limulus* moults a submarginal suture opens in front, and after the animal has crept out, the suture closes leaving a perfect "complete specimen" to be preserved. An experiment with dead individuals and moults of *Limulus* kept in an aquarium together with living shrimps and other forms indicates that the empty moults have a far better chance of preservation than the dead individuals. The shrimps attacked and disrupted the dead *Limulus* but left the moults untouched (STØRMER 1934: 57). Under anaerobic conditions, however, a scavenging bottom fauna would be absent, and dead individuals which occasionally drifted into the hydrosulphid water above the bottom could be well preserved.

A great number of entire specimens of *Eurypterus remipes* and *Baltoeurypterus tetragonophthalmus* have been preserved in calcareous muds with a high magnesium content, the so-called waterlimes (KJELLESVIG-WAERING 1958: 1107). In their study of the growth and variation in *Eurypterus remipes*, ANDREWS et al. (1974: 88) assume that these eurypterids lived in subtidal lagoons with somewhat hypersaline water. They think it possible that the occurrences represent a mass death of eurypterids living near the shore, that the eurypterids were buried in a catastrophic fashion. In support of this view they point to the complete preservation of entire specimens with all the appendages and eye integument intact, and the occurrence of one specimen completely disarticulated but with all segments aligned and all the appendages preserved is "thus evidencing the absence of post-mortem disturbances by currents and scavengers". A second specimen oriented upside down on the bedding plane with its telson penetrating the underlying sediment, is tentatively interpreted as an individual in the act of rightening itself. In rare cases a mass death of eurypterids as suggested by the authors mentioned may have happened if the eurypterids were trapped in shallow water lagoons behind the tidal flats. In such low energy environments heavy rainfall alternating with strong evaporation during dry periods may have caused too great a variation in salinity for the survival of the eurypterids even if they were euryhaline (see p. 133).

The points mentioned, however, may also be explained by assuming the presence of shed moults rather than dead bodies. Shed moults of *Limulus* with all finer details and with the eye integument present appear, as far as I can make out, as "complete specimens". As in Recent *Limulus* one would expect to find certain disarticulated fossil exuviae, some of them lying on their backs with the telson partly penetrating a soft mud. If the numerous entire specimens of *Eurypterus remipes* of Fiddlers Green N.Y. and of *Baltoeurypterus tetragonophthalmus* of Saarema/Estonia represent dead bodies, one would expect to find traces of the gut infillings such as in the Burgess Shale fossils and in a specimen of *Arthropleura* described by ROLFE (1969: *R* 615). In eurypterids an impression of the intestine is known in one specimen of *Carcinosoma newlini* only (RUEDEMANN 1921: 92, text-fig. 3). ANDREWS & al. (1974) admit the presence of isolated preserved parts of eurypterid specimens belonging to moults, but the evidence available seems to me rather to indicate that most eurypterid specimens preserved are shed moults or exuviae.

The eurypterid material from Alken offers some information on the present subject. Transport by currents of the eurypterid specimens is demonstrated in most specimens of *Drepanopterus struvei* (STØRMER 1974: text-figs. 18-19), *Alkenopterus brevitelson* (STØRMER 1974: text-figs. 21-22) and *Moselopterus ancylotelson* (STØRMER 1974: text-figs. 24-27). In all these specimens the tail is bent outwards and forwards, in certain cases up to 180°, so that the metasoma becomes parallel to the mesosoma. Such a strong bend of the abdomen would hardly be possible in dead animals with limited lateral flexibility. The positions indicate transport of an empty exuvia and may be called a current position of the body. The holotype of *Moselopterus elongatus* (STØRMER 1974: text-fig. 27a) has an open marginal suture marking the presence of an empty exuvia. The current position of the abdomen is not characteristic of the many specimens of *Parahughmilleria hefteri* and *P. major*. Whether this is due to a

more solid connection between the plates in the moults or the possible presence of dead bodies, cannot be ascertained, but the lack of any traces of a gut infilling suggests the first interpretation.

Composition of the arthropod fauna.

Associated flora and fauna.

Before we discuss the arthropod fauna it is necessary briefly to mention the other fossils occurring in the dark shale of Alken.

In his valuable paper on "Die Hunsrück-Insel im oberen Unterdevon" SOLLE (1970) describes the stratigraphy of the fossiliferous beds of Alken and at the same time mentions all the fossils known, with remarks on their probable ecology. He emphasizes, however, that a complete description of the flora and fauna is far from finished.

Among the aquatic plants the Thallophyta are represented by the genera *Chaetocladus* and *Thamnocladus*. Psilophytes are very common, also specimens with sporangia. Characteristic is *Taeniocrada* which occurs in great quantities and may even form coal (SOLLE 1970: 347). According to KRÄUSEL & WEYLAND (1930: 36) *Taeniocrada decheniana* was a waterplant. SCHAARSCHMIDT (1970: 36), however, assumes that this psilophyte might have been more terrestrial and had an upright grass-like growth. At best the fertile shoot reached above the water. *Zosterophyllum rhenanum* was perhaps a more typical waterplant. Mr. HEFTER has recorded a stem with a diameter of 12 cm, which SCHAARSCHMIDT (1975) described as belonging to a new genus, *Mosellophyton hefteri*: According to SCHAARSCHMIDT this thick-stemmed plant might have been a succulent halophyte living near the shore-line of the lagoon where the water occasionally changed from fresh to brackish and salty. Parts of the plant were probably above water. SCHAARSCHMIDT suggests the possibility that the oldest kormophytes might have been halophytes. The present studies indicate that the degree of salinity was subject to changes in the lagoon, and the tide might also have caused problems to a plant in the intertidal zone. In invading the land under such conditions it would have been favourable to the plant to have been succulent and euryhaline.

The non-arthropod invertebrate fossils comprise mainly Bivalvia. Characteristic is the large oyster-like *Limoptera* (*Klinoptera*) *rhenana* which is regarded as a marine form. However, the Bivalvia and Gastropoda occuring in the dark sediments are mainly "Kümmerformen" in which the shell is prediagnetically dissolved probably due to a decreased salinity (SOLLE 1970: 62). *Tentaculites* occurs and *Spirorbis* has been noticed on the shell of a bivalve. I have noticed certain, larger shell fragments with a corrugated surface which possibly belong to a nautiloid. Furthermore there are small silicified bodies which have been determined as Foraminifera by JENÖ NAGY, curator at the Institute of Geology, University of Oslo. The presence of "*Lingula*" and *Leperditia*-like ostracods may indicate brackish water.

The vertebrates are represented by the ostracoderm *Rhinopteraspis dunensis*, which is characteristic of the Lower Devonian over a large area of Europe, and *Drepanaspis* (arthrodire) and *Porolepis* (crossopterygian).

The fossils mentioned were probably euryhaline indicating both marine and brackish conditions.

The arthropod fauna.

The arthropods described in part 1-5 are almost all new species. Some of them may be endemic of the Rhine area, but since our present knowledge of dark shale arthropods of the Lower Devonian is very limited, future finds may show that members of the fauna had a considerably wider distribution than we know at present.

Identical or related species have been described from other localities in the Rhine area (STØRMER 1973: 121; WEIDMANN 1967).

As indicated in the list table 2 only the two species of *Parahughmilleria* are common. A few, such as the eurypterid *Moselopterus ancylotelson* and the xiphosurid *Diploaspis* are not rare, at least in certain portions of the collected material. All the other species are very rare, in many areas represented by one specimen only.

Table 2. List of arthropods from the Nellenköpfchen-Schichten of Alken an der Mosel. — In the list the publication, the approximate average length in mm of the adult body and roughly the abundance (c = common; cc = very common) or the rarity (r = rare; rr = very rare) of the species are indicated.

Taxa	publication	body length	frequency
Eurypterida:			
Parahughmilleria hefteri	STØRMER 1973	70	cc
Parahughmilleria major	STØRMER 1973	85	c
Jaekelopterus rhenaniae	STØRMER 1976	— 1800	rr
Drepanopterus struvei	STØRMER 1974	? 75	rr
Alkenopterus brevitelson	STØRMER 1974	? 65	rr
Moselopterus ancylotelson	STØRMER 1974	130	cr
Moselopterus elongatus	STØRMER 1974	135	rr
Wilwerathia laticeps	STØRMER 1974	?? 100	rr
Rhenopterus macrotuberculatus	STØRMER 1974	?? 80	rr
Carcinosoma sp.	STØRMER 1974	? 200	rr
? Stylonuridarum g. et sp. indet.	STØRMER 1974	?	rr
Eurypteridorum g. et sp. indet.	STØRMER 1974	?	rr
? Eurypterida:			
Thurandina waterstoni	STØRMER 1974	?	rr
Xiphosura:			
Diploaspis castori	STØRMER 1972	16	cr
Heteroaspis novojilovi	STØRMER 1972	? 20	rr
? Merostomatidorum g. et sp. indet.	STØRMER 1976	?	rr
Arachnida:			
Waeringoscorpio hefteri	STØRMER 1970	? 21	rr
Scorpionidorum g. et sp. indet.	STØRMER 1974	? 40	rr
Alkenia mirabilis	STØRMER 1970	12·5	rr
Archaeomartus levis	STØRMER 1970	? 6	rr
Archaeomartus tuberculatus	STØRMER 1970	? 9	rr
Archaeometa ? devonica	STØRMER 1976	? 18	rr
Myriapoda:			
Eoarthropleura devonica	STØRMER 1976	?? about 100	rr
Arthropoda incertae sedis:	STØRMER 1976	? 6	rr

Size groups.

The sizes given in table 2 are not very reliable. Often some part of the body is missing and we do not know whether young or adult specimens are present. Thus, the specimen present of *Jaekelopterus rhenaniae* probably had a body length of about 160 mm whereas the largest specimen known may have been 1800 mm long (STØRMER 1936: 52).

Although the measurements are very uncertain it seems possible to distinguish certain size groups.

(1) Length 6-20 mm: This group comprises all the arachnids except the scorpions of which the length of the two specimens were probably 21 mm and ?40 mm.
(2) Length 65-85 mm: Here we have the smaller eurypterids *Hughmilleria*, *Drepanopterus* and *Rhenopterus*.
(3) Length 100-135 mm: This group includes the medium-sized eurypterids *Moselopterus* and *Wilwerathia* and probably the "centipede" *Eoarthropleura*, the length of which, however, is very uncertain.
(4) Length > 200 mm: The largest forms are represented by *Jaekelopterus* and *Carcinosoma*.

Larval stages, not included in the groups, are fairly common in *Parahughmilleria*, but the earlier instars are missing as discussed below. It may be worth mentioning that in a small collection sent to me by the late Mr. HEFTER six small specimens of *Parahughmilleria*, probably from one split piece of shale, had an estimated body length which varied only from 11·5 mm to 15 mm. These six larval specimens may possibly have belonged to one shoal of young eurypterids.

Palaeoecology of the Alken arthropods.

In their excellent study of Upper Carboniferous black shales ZANGERL & RICHARDSON (1963: 3) recall that both palaeoecology and neoecology investigate the complex relationships of organisms and environment, but while the latter is determined by direct observation and determinations, the former is based on indirect evidence only.

The mixed arthropod fauna of the Nellenköpfchen-Schichten evidently represents different biological niches. In order to obtain a general picture of the fauna in and around the ancient lagoon or channel it is necessary to try to determine the mode of life of the various members of the arthropod fauna. The analysis has to be based chiefly on morphological characters and the associated fauna.

Eurypterida.

Previous authors have pointed out the difference in the development of the last pair of prosomal appendages, a feature indicating either benthonic or partly nectonic forms. However, with regard to their relationships to the environment the eurypterids have usually been treated as one common group living largely in the same environment. However, with his extensive knowledge of eurypterid faunas KJELLESVIG-WAERING (1961: 793, 1966: 1110) distinguishes three different main assemblages of eurypterids: (1) Carcinosomatidae-Pterygotidae, (2) Eurypteridae, (3) Hughmilleriidae-Stylonuridae.

With the eurypterid classification suggested by STØRMER (1974) the names of the groups may be slightly modified:

(1) Carcinosomatidae-Pterygotoidea,
(2) Eurypteridae,
(3) Hughmilleriidae-Drepanopteridae-Stylonuroidea.

The two first assemblages occur together with marine forms such as graptolites, starfishes and others, and may be regarded as marine-brackish. Faunas of the last group which do not include marine forms, must be regarded as brackish to fresh-water assemblages. Transition assemblages naturally occur.

The characteristic waterlime faunas of New York State and Estonia belong to group 2. It is possible that hypersaline water conditions may favour this biofacies.

The Alken eurypterid fauna evidently belongs to group 3. Hughmilleriidae are most abundant, and most of the other eurypterids are Drepanopteridae and Stylonuroidea. However, the few specimens of *Jaekelopterus*, belonging to the Pterygotoidea, and *Carcinosoma* indicate a certain mixture of assemblages.

Parahughmilleria hefteri and *P. major* were evidently excellent swimmers. Although the known occurrences suggest that they preferred brackish water, the wide distribution of the genus indicates that they were euryhaline, being able to cross purely marine waters. The great number of specimens of the two Alken species shows that they were the main and permanent members of the lagoon fauna. The medium-sized chelicerae suggest that they might have been predators. The large *Jaekelopterus* was also an able swimmer, and at the same time a pronounced predator. Probably single individuals of this species visited the lagoon as did the sharks in the Carboniferous ponds described by ZANGERL & RICHARDSON (1963: 195).

Characteristic of the drepanopteroids and the stylonuroids is the lack of paddles (a slight tendency towards the development of such organs is seen in *Moselopterus*). The well developed walking legs show that these eurypterids were benthonic forms. The powerful distal spines on the legs suggest that they were adapted for walking on sand or solid ground rather than soft mud or clay. In *Moselopterus* (STØRMER 1974: 399) the relatively large posterior pairs of prosomal appendages indicate that the opisthosoma could be raised considerably as in Recent scorpions. The short curved telson might have served as a weapon and could also have been used to anchor the animal to plants and other fixed objects in order to avoid being drifted away by surf or currents along the shore. With the flat scorpion-like body and the morphological structures mentioned, *Moselopterus* may also have been fitted for walk on land. As mentioned in a later chapter (p. 143) the ventral plates protecting the gills, and the peculiar trachea-like structures in *Baltoeurypterus*, indicate that many eurypterids might have been partially terrestrial, being able to stay for a considerable time in the supratidal zone, or endure the drying up of the pond in shorter periods.

Drepanopterus and *Alkenopterus* also have short telsons, though not curved. The legs suggest a similar mode of life similar to that of *Moselopterus*. All three genera show the characteristic current position of the preserved specimens interpreted as exuviae. The drepanopterids mentioned were probably amphibious forms living partly on the sandy and muddy beaches, in the "mangroves"

and on the land beyond. Moults occasionally shed in the intertidal zone were caught by the surf and tidal currents and transported into the deeper and more anaerobic part of the lagoon or channels where the skins became preserved. *Wilwerathia* and *Rhenopterus* may also have belonged to the niche occupied by the drepanopterids.

With their well protected gills even the parahughmilleriids might to some extent have been able to crawl on land in the intertidal zone. Little can be said about the single fragment of *Carcinosoma* sp.

Larval stages of *Parahughmilleria* occur but the earliest instars are missing. The smallest larva of *P. hejteri* measures 7·5 mm in body length (STØRMER 1973: 165, pl. 10 fig. 3); the shape of the body hardly indicates an early instar. The absence of early instars is characteristic also of the *Eurypterus remipes* and *Baltoeurypterus tetragonophthalmus* faunas. According to ANDREWS & al. (1974: text-fig. 4) the earliest instar of *E. remipes* presented in the graph has a prosomal length of 0·68 mm, corresponding to a body length of 37 mm. Very early instars of eurypterids are only known in *Stylonurus myops* (CLARKE & RUEDEMANN 1912: 304, pl. 57 figs. 1-4). The smallest specimen measuring about 1·5 mm only, probably represents one of the very first instars. It is interesting to ascertain that the small instars of *S. myops* come from the Shawangunk Grit which comprises "heavy beds of conglomerate with very thin shale seams between". The Recent *Limulus* crawl up on the sandy or muddy beach and lay their eggs within the tidal zone. Organic remains in such arenaceous beds have not the same chances of preservation as have remains in anaerobic and hypersaline (?) muds. The eurypterids might have laid their eggs in a similar environment, and this might be the reason for the lack of early instars in the non-arenaceous sediments.

The analysis of the eurypterid fauna indicates that the water of the Alken lagoon was mainly brackish, a conclusion which agrees with the other non-arthropod fossils. However, the eurypterid fauna hardly reflects conditions resulting from one balanced eco-system. The pterygotids were probably casual intruders and the drepanopterids were probably not permanent inhabitants of the lagoon.

Xiphosura.

The quite small *Diploaspis* and *Heteroaspis* with their large ventral shield protecting the gills may also have been partly amphibious forms. They probably lived in the psilophyte "mangroves" where they might have managed to live and climb on the plants partly submerged and partly above the water (STØRMER 1972: 12).

Arachnida.

Three orders, the Scorpionida, Trigonotarbida and Araneida, are represented in the fossil fauna. *Waeringoscorpio* (text-fig. 83) probably had well developed gills indicating that it was aquatic and belonged to the fauna of the lagoon. The habitat of the other scorpion (text-fig. 47) can not be determined from the specimen preserved.

The smaller arachnids representing the Trigonotarbidae and Araneida were evidently terrestrial like the related forms from the probably Lower Devonian Rhynie Chert bed and various Carboniferous deposits (STORMER 1970). The undetermined arthropod described above (text-fig. 55) may have belonged to the same niche.

Myriapoda.

The general resemblance of *Eoarthropleura* and *Arthropleura* indicates that these "centipedes" had a similar mode of life. The flat head (probably present also in *Arthropleura*) and the flat body facilitated movements among plant debris. They might have been amphibious, or at least lived in the swamps in a humid environment. The smaller Devonian species with the broad doublure and longer legs was probably the more agile.

Conclusions.

The arthropod fauna of Alken is a composite one, including a diversity of species and habitats. The similarities between these Lower Devonian species and those living in Upper Carboniferous swamps some 70 million years later are very remarkable.

Palaeoecology of the Nellenköpfchen-Schichten of Alken.

Local stratigraphy and sedimentology.

According to SOLLE (1970: 55) the dark shales of the Alken section comprise two main horizons separated by arenaceous beds, the "Unterbank" and the "Oberbank", the latter about 20 m above the former.

The Unterbank [Lower Layer] (0·7-1·5 m) has the most important plant-bearing beds. Certain mass occurrences of a psilophyte and algal remains closely resemble the bands ("Spülsäume") of plant debris on Recent beaches. The large bivalve *Limoptera (Klinoptera) rhenana*, eurypterid remains and the one specimen of the scorpion *Waeringoscorpio hefteri* have been found in the lower bank. Plant fragments occur in a bed about 0·5 m above the typical Unterbank.

The Oberbank [Upper Layer] (3-3·5 m) has alternating beds of shale, silt and sandstone. *Limoptera* occurs only in the lowermost 0·5 m and eurypterids are relatively abundant in the middle part where terrestrial arachnids also occur. The ostracoderm *Rhinopteraspis dunensis* evidently belongs to the Oberbank (FAHLBUSCH 1966; HEFTER 1973). The abundant plant remains include sporangia and spores.

The greywackes, the cleaner sandstones and siltstones which constitute the main part of the Alken section have been studied with regard to sedimental structures by NIEHOFF (1958). Clayballs occur in the arenaceous beds and mud-cracks and vertical borings may continue into the shale. Detailed studies of the

contemporaneous Nellenköpfchen-Schichten from the Nellenköpfchen at Ehrenbreitstein about 20 km NE. of Alken, have been carried out by WUNDERLICH (1970). These sediments consisting of alternating clay-, silt- and sandstones show well preserved sedimentary structures similar to those of the extensive tidal flats (Watt) along the southern coasts of the North Sea. WUNDERLICH assumes that the sediments at Ehrenbreitstein were deposited along an oceanic shore where the magnitude of the tide might have been at least 2-3 meters.

From a careful analysis of the Mosel-Rhein area SOLLE (1970) concludes that during the upper Lower Devonian an extensive Hunsrück-Island existed bordered by tidal flats with the occasional development for short periods of lagoons (at Treis and Alken). Marine and brackish animals inhabited the lagoons and "mangroves" along the flat shores.

Before we discuss the palaeoecology of the Nellenköpfchen-Schichten at Alken we may mention a largely contemporaneous and rather similar biota and environment. The famous Lower Devonian (possibly Emsian) flora and fauna of the Rhynie Chert Bed of Aberdeenshire in Scotland has no marine fossils. According to KIDSTONE & LANG (1921: 596) the deposits were formed in a gradually subsiding marsh or lake. The plant beds alternate with layers of sand. The arthropod fauna consists of terrestrial arachnids related to those of Alken (HIRST & MAULIK 1936; SCOURFIELD 1940), Collembola (SCOURFIELD 1940) and an aquatic crustacean (SCOURFIELD 1940).

Attempted reconstruction of life and environment.

A reconstruction of life and environment of the arthropod fauna of the Nellenköpfchen-Schichten at Alken has to be based on the following evidences:

(1) The dark fossiliferous sediments occur as pockets or lenses in the coarse sediments deposited along the shores of the Hunsrück Island situated close to the Lower Devonian equator.

(2) The argillaceous beds representing protected low energy conditions were deposited landwards from the exposed sandbars.

(3) The arthropod fauna includes marine and brackish water species as well as amphibious and terrestrial forms.

Since both nektonic and benthonic marine forms were present in the basin some connection with the open sea existed. Because of the small current activity indicated by the fine sediment the mud was evidently deposited in an estuary or lagoon.

Recent estuaries and lagoons have been treated by EMERY & STEVENS (1957). Since the Alken beds were deposited along the coast of the Hunsrück Island we would hardly expect the presence of a large river producing an extensive estuary. Lagoons, however, are common along coasts and are separated from the ocean by offshore bars or islands. The lagoons have areas of quiet water, and in tropical regions vegetation of the tidal flats generally forms mangrove swamps. In the lagoons the entrance is restricted, often forming channels.

Although the tropical "mangroves" are missing, the Wadden Sea or Watt along the Dutch-German coasts has formations and deposits which may have a significant bearing on the structures observed at Alken (REINECK 1970: text-fig. 56). Because of the considerable tidal range (2-3 m) and a rapid supply of sedi-

ment the intertidal zone is very broad and pierced by deep channels leading the water away when the tide drops. Lagoons are often present near the upper margin of the tidal flat. The salinity of the water in these lagoons varies to a considerable extent. In times of dry weather the salinity increases by evaporation and in rainy weather more brackish water is formed. Through the channels marine animals may enter the lagoon and euryhaline forms may be more permanent inhabitants.

Along the East Coast of N. America numerous ponds occur which at times during the postglacial eustatic rise of the sea level had access to the sea. Studies by EMERY (1969) on the Oyster Pond of Cape Cod, using advanced methods including borings and radiometric dating, are of interest in interpreting the Alken sediments and organic remains. In the pond sessile water plants grow down to 1 m along the shores. During the summer masses of these plants break away from the bottom, drift away and sink to the bottom where they contribute to the organic matter of the sediments. The bottom layer of the water of the pond has hydrogensulfide and the bottom sediments in the middle of the pond consist of fine organic silt (approaching the grain size of clay). When the pond had access to the sea (now closed by a sand bar) marine oysters were present.

Because of the rapid supply of organic carbon and lack of bioturbation, the dark sediments at Alken probably were deposited under anaerobic conditions like those in the pond. The presence of marine animals such as the oyster-like *Limoptera* and the existence of the nectonic and far-travelling *Parahughmilleria* and *Jaekelopterus* show that the ancient lagoon or sound had access to the open sea. The lack of disturbed bottom sediments may suggest that these parts were not affected by strong tidal currents. The arenaceous beds representing the exposed beaches have trails and tracks but practically no fossils, although animal life probably flourished. Lack of fossils is evidently a matter of preservation only.

ZANGERL & RICHARDSON's (1963) study on life and environment in an upper Carboniferous pond may also be mentioned in connection with the Alken fossils. In a peat-swamp floating mats drifted around in the lagoons, and plants and animals were deposited. Many tests of crustaceans which were badly shrivelled (ZANGERL & RICHARDSON 1963: 128) were tentatively interpreted as freshly moulted individuals. As mentioned above (p. 123) the similar preservation of Alken eurypterids may rather be interpreted as due to a dissolution of the calcareous component of the test. It is interesting to notice that the pond was occasionally visited by large predators such as sharks. Similar conditions may have existed in the Alken lagoon where fragments of the large *Jaekelopterus* indicate occasional visits of this predator. ZANGERL & RICHARDSON (1963: 195) point out that the general conditions "strongly suggest that the Mecca and Logan Quarry environments do not reflect conditions from balanced eco-systems". The same may be said of the Alken Quarry environment.

Conclusions.

A comparison with Recent and fossil environments seems to permit a rather detailed interpretation of the landscape and life at the Alken Quarry in Lower Devonian (Emsian) time. The results presented confirm and add new details to the general interpretation presented by SOLLE (1970). Along the coast of SOLLE's Hunsrück Island, we probably had an elongate lagoon bordered by a sandy bar

with a broad tidal flat with certain water channels communicating with the otherwise landlocked lagoon. Salt water entered the lagoon at high tide and because of its weight mingled with the bottom water of the lagoon. The salinity of the lagoon varied with evaporation and rainfall. Round the pond we had swamps with psilophytes and other primitive land plants. Some of the plants lived partly emerged in the pond with the shoots just above the water. Typical water plants were also present. On land terrestrial arachnids crawled on the plants and dry surfaces in the swamps, and probably the centipede *Eoarthropleura* lived an amphibious life among plants and plant debris at the shore and in the swamp. The small xiphosurans were mainly aquatic but could also crawl about on the beach and perhaps settle on the shoots of the plants sticking up of the water. The stylonuroid eurypterids were probably also amphibious in the sense that they were able to stay at times on land.

In the lagoon the permanent members such as the bivalves, were marine and euryhaline. The able swimmers such as the eurypterid *Parahughmilleria* and probably also the ostracoderm *Rhinopteraspis* might have been able to swim in and out of the lagoon. The large carnivorous *Jaekelopterus* probably paid occasional visits into the lagoon looking for suitable prey. The other eurypterids lived partly in the lagoon and partly in the swamps and on the beaches. The general field setting and the varied animal life evidently offered the best opportunities of an invasion of the land by various arthropod groups as discussed in the next chapter.

The problems of arthropods invading the land.

The Lower Devonian sediments and fossil remains from Alken have made it possible, at least to some extent, to reconstruct the environment and life which prevailed in this area at this particular time. We may envisage a varied landscape of sheltered lagoons, often with stagnant waters and extensive "mangroves", partly bordered by muddy and sandy beaches. The Lower Devonian and the later Silurian times are of particular importance to the history of life. At this time plants and animals of the sea, lakes and rivers were on their way to invade and conquer the land. The swamps, the early "mangroves" and the beaches with an abundance of plant litter were the "land of promise" for the animals struggling for life in the less nutritive waters along the shores.

Of late years considerable interest has been devoted to the problem of adaptations of aquatic arthropods to terrestrial life. A symposium on "Terrestrial adaptations in Crustacea" was held in New York in 1967 and several papers from that Symposium are cited below.

The term "terrestrial" is defined by HURLEY (1968: 327) as "being independent of the sea or of standing bodies of water for breeding, feeding and distribution". However, there are many transition stages between a true aquatic habitat, through various degrees of amphibious to a true terrestrial mode of life.

The main advantages connected with an invasion on the land were (1) to obtain new areas rich in food, (2) to escape enemies and (3) to have their youngsters protected from the predators of the sea.

Horseshoe crabs and marine turtles crawl ashore to lay their eggs deep in the sand of the beach where they are well protected. As pointed out by ROMER (1966: 86, 102) the appearance of the amphibians on land "seems, curiously, to have resulted from adaptations primarily useful in aiding them to survive in the water". In terrestrial decapods the female carries the eggs, and the larval development takes place either in water (as in amphibians) or within the egg (as in reptiles) (BLISS 1968).

The invasion of the land took place more or less simultaneously in plants and arthropods. The vertebrates probably arrived a little later. Among the arthropods the invasion evidently started with brief excursions into the intertidal and supralitoral zones of the beaches. Certain groups could stay out of water for some time if they were able to avoid desiccation, particularly of the gills. Other groups successfully found very wet environments on the land and thus avoided desiccation. Those who were able to master the difficulties could gradually develop or modify certain organs in order to meet the new conditions.

The various arthropod groups used different routes in their approach of the land. As pointed out by DOROTHY E. BLISS & LINDA HABAS MANTEL in the summary of the Symposium (1968: 674) the invaders came "across sandy beaches or the rocky intertidal zone, through mangrove swamps or by the way of freshwater lakes or streams". The first routes would mean very abrupt change in environment, a change which would leave very short time for adaptations. If, however, the arthropods were able to use the "back door" and find their way through the wet plant debris on the shore, an environment they could maintain for a long time, a gradual adaptation would have time to develop.

Zoologists often regard the large terrestrial groups, particularly the Myriapoda and Insecta (Hexapoda), as primary terrestrial. MANTON (1973: 260) assumes that the terrestrial ancestor of the myriapods and insects "must have been moderately soft bodied, possessing tendencies towards cephalization and equipped with lobopodal unjointed limbs. Presumably they left the sea with these features during the Silurian, or whenever their invasion of the land took place. . . . The Uniramia [Onychophora, Myriapoda and Insecta], before they left the sea, stood in marked contrast to contemporary Crustacea and Chelicerata which possessed well armoured bodies, jointed trunks and limbs." However, the early myriapods from the Silurian and Lower Devonian which had a solid exoskeleton might have been aquatic or amphibious animals not much different from the later terrestrial forms. In my opinion the major arthropod groups might have had well developed exoskeletons and limbs before they left the sea.

Adaptations to terrestrial life.

LAWRENCE (1953: 123) quotes WIGGLESWORTH (1933) in saying that "Terrestrial life is a perpetual conflict between the need of oxygen and the need of water; for those conditions which favour the entry of oxygen into the body, favour also the escape of water".

The main morphological-anatomical adaptations to terrestrial life comprise:
(1) structural changes to avoid desiccation of body (see below),
(2) modifications of existing and development of new respiratory systems (see below),
(3) modifications of morphological characters related to movement (p. 152),
(4) modifications of sensory organs (p. 153) and
(5) development of a preoral cavity in relation to feeding and digestion (p. 154).

The last point has as far as I know not previously been emphasized. As pointed out below this structure seems to be necessary for a complete adaptation to terrestrial life.

There are also a variety of physiological, biochemical and behavioural adaptations (BLISS & MANTEL 1968: 674) and adaptations to changes in temperature, which cannot be traced and assessed by the palaeontologist.

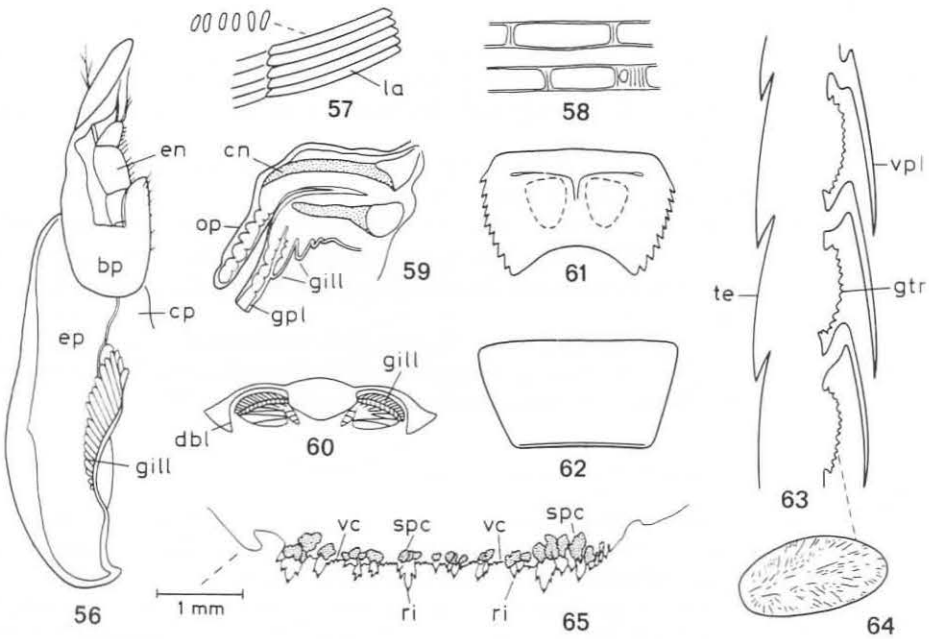
Structural changes to avoid desiccation of body.

The arthropod body is covered by an integument which is either soft and flexible or hardened into sclerites forming an exoskeleton. The hardness of the cuticula is not dependent on the amount of chitin, but is due to an impregnation of quinone-tanned proteins or calcareous substances (the latter present in crustaceans and diplopods) (KÄSTNER 1968: 39). The cuticula is generally composed of a thick procuticula which is covered by a very thin and practically nonchitinous epicuticula. While the procuticula is very resistant to physical and chemical agents, the wax- and lipoid-containing epicuticula is unpenetrable by water and, thus, is of primary importance in avoiding a desiccation of the body. If such an epicuticula is lacking, the arthropod has to live in a damp environment and to keep the body-surface constantly wet as do the amphibians among the vertebrates.

Modification of existing and development of new respiratory systems.

Detailed studies of Recent terrestrial arthropods have demonstrated many different ways in which aquatic forms have adapted their respiratory organs to the new mode of life. Largely the adaptations have developed along two main lines, either an adjustment of the existing gills or the formation of lung-like structures. Respiratory adaptations occur in the Merostomata, Arachnida, Crustacea, Myriapoda and Insecta. Text-fig. 107 indicates the main adaptations and their occurrences in the various groups.

Before we discuss the various types of respiratory organs it is worthwhile to mention the branchial structures in the Trilobita and Trilobitoidea. In previous papers (STØRMER 1939, 1959) I have advocated the view that the filaments of the exites of the appendages served as gills. In a recent paper BERGSTRÖM (1973: 57, 61) doubts their gill function and believes that they were mainly used for "scratching in the sediment surface" and that they "may have been used in swimming". He suggests that the gas exchange may have taken place through the whole ventral surface between the lateral doublures (as mentioned below, respiration in decapodes takes place through the vascular



Text-figs. 56-65. Respiratory structures in aquatic arthropods. — Not drawn to scale. — bp = basipodite; cp = coxopodite; dbl = doublure; cn = cartilage; en = endopodite; ep = epipodite; gpl = gill plate; la = lamella; op = operculum; ri = ridge; spc = spongy chitin; vc = venous canals; te = tergite; vpl = ventral plate.

Text-fig. 56. Respiratory organs in Cumacea: *Diastylis bradyi* Norman 1888. Mandible with gill on the epipodite.

Text-fig. 57. Respiratory organs in Trilobita: Gill lamellae with distal spines or setae, and cross-section of lamellae.

Text-figs. 58-62. Respiratory organs in Xiphosura:

58-60. *Limulus polyphemus* (Linnaeus 1758). — 58: Cross-section of gill-lamellae showing supporting pillars (after Gerhard 1935 from Versluys & Demoll 1922). — 59: Longitudinal section of embryo showing operculum and first gill-bearing abdominal appendage or plate. Five primordial gill-lamellae are developing at the base of the ventral plate (simplified from Wills 1965 after Patten & Hazen 1900). — 60: Cross-section of abdomen showing position of gill-appendages.

61. *Chasmataspis laurencii* Caster & Brooks 1965. Ventral abdominal plate with outlines of gill-tracts (?) (after Caster & Brooks 1956).

62. *Diploaspis casteri* Størmer 1972. Ventral abdominal plate (after Størmer 1972).

Text-figs. 63-65. Respiratory organs in Eurypterida: *Baltoeurypterus tetragonophthalmus* (Fischer 1839). — 63: Longitudinal section of mesosoma showing dorsal tergites, ventral plates and gill tracts. — 64: Gill-tract (comp. text-fig. 65). — 65: Cross-section of gill-tract, reconstruction (after Wills 1965).

lining of the branchial chamber). The narrow lamellae of the fringe are regarded more like strong cylindrical spines than lamellae with a subrectangular cross section (text-fig. 57). The lamellae had a certain flexibility as shown by RAYMOND (1920: pl. 9 fig. 2) and STØRMER (1939: 211). Only the distal portion of the lamellae is provided with a cylindrical spine or fixed seta. This distal portion of the fringe might have been used in scratching, especially in forms like *Ceraurus* with a free distal portion of the branch; in *Olenoides*, *Cryptolithus* and *Triarthrus*, however, the posterior portion of the main part of the fringe was covered in ventral view by the front of the following appendage and could therefore hardly have served in scratching or swimming. The swimming might have been performed largely by the telopods; in *Limulus* both the prosomal telopods and the appendages of the abdomen take part in swimming.

We do not know the internal structures of presumed branchial lamellae, but gill-blades in Xiphosura (text-fig. 58) and in Isopoda (text-figs. 77-78) have internal vertical pillars keeping the two opposing walls in position. A special filter function of the lamellate fringe might have been present in trilobites, but hardly in some of the trilobitoids. In my opinion our present knowledge indicates that the lamellae of the fringe of the exite (epipodite or preepipodite) mainly served as gills. Lamellate gills analogous to those in trilobites occur in the Cumacea of the Crustacea (text-fig. 56).

There are no reasons to believe that the trilobites or trilobitoids invaded the land. In the following, arthropods more or less adapted to terrestrial life are briefly treated with regard to their various adaptations to the new mode of life.

Xiphosura.

The living horseshoe crabs go ashore for shorter times during the spawning season. Their stay on land is limited to the intertidal zone of the beaches or to the river banks where they crawl about on the sandy and muddy flats where they are able to stay out of water for a considerable time. This is possible because the gills are kept wet all the time. The gills are covered ventrally by extensive plate-shaped appendages, and laterally by the bulging doublures of the abdominal shield (text-fig. 60). This arrangement which we may call the *Limulus*-method of protecting the gills, is found in several different arthropods (text-fig. 82).

From an analogy with *Limulus* we may assume that fossil arthropods with one or more extensive ventral abdominal shields possessed more fragile structures above which was needed protection both against damage and or desiccation. One ventral shield or a set of protecting plates are found in many fossil forms such as in the Ordovician *Chasmataspis* (CASTER & BROOKS 1956) (text-fig. 61) which also show the outlines of the gill-sacs (?), and in the Lower Devonian *Diploaspis* (text-fig. 62) and *Heteroaspis*, both from the Alken fauna (STØRMER 1972). Furthermore, the many eurypterids (text-fig. 63) and Palaeozoic scorpions (text-figs. 83-85) have separated or fused ventral plates opening backwards. Also in several Recent arachnids (e. g., in the spiders) the anterior ventral plates have entrances to the book-lungs along the posterior border. In Recent scorpions the openings have secondarily moved forwards forming the stigmata, as mentioned below.

Eurypterida.

Although gill-structures were claimed to be found by WOODWARD (1866-1876) in *Erettopterus* and *Slimonia*, the first description of true gills were presented in HOLM's (1898) excellent study of *Baltoeurypterus* [*Eurypterus*][2]). MOORE (1941) restudied *Slimonia* and was able to show that the gills belong to the ventral body wall, rather than to the dorsal surface of the ventral plates as generally assumed. WATERSTON (1975) has made further careful studies of the gills in *Tarsopterella*, his results being presented at the Trilobite-trilobitoid-merostome Symposium in Oslo 1973.

Unfortunately HOLM's studies on the gill-structures of *Baltoeurypterus tetragonophthalmus* [*"Eurypterus fischeri"*, e. p.] and *Erettopterus osiliensis* were not completed, but a number of plates with excellent drawings by Mr. G. LILJEVALL were printed about 1920–21. It is the merit of WILLS (1936) to have completed the important studies initiated by HOLM. WILLS' thorough and detailed studies of many of HOLM's type specimens confirm the structures demonstrated in HOLM's plates.

The gills comprise five pairs of elliptical areas or "gill-tracts" on the lower surface of the mesosoma (preabdomen). They are well protected by the ventral plates below (text-fig. 63). On the surface of each gill-tract WILLS distinguishes what he calls "ridges" and "valleys". They appear in a treetrunk-like pattern, the trunks ramifying inwards towards the median line (text-figs. 64 and 66). The arrangement is very similar to structures in terrestrial isopods (text-fig. 81).

In transmitted light the valleys are lighter than the ridges, suggesting empty spaces or lacunae above them (text-figs. 66-67). The whole surface of the gill-tract is covered by minute cone-shaped pustules or spinules (text-fig. 68). The small pustules are shorter in the valleys than on the ridges. Each pustule has a cone-shaped solid spine on the top (possibly lacking on some of the pustules in the valleys). The surface consists of very small polygons bordered by narrow chitinous bars or ribs with a rosette-like structure at the meeting-point of the bars (text-figs. 69-70). Each rosette is flat on the top and has a quite short stalk or peduncle. In *Erettopterus* setae occur at the corners of the polygons (WILLS 1965: pl. 1 fig. 11).

While the bottoms of the valleys are flat and even, the ridges show a corrugated structure composed of a number of parallel steep ridges separated by deep and narrow folds or invaginations (text-figs. 65, 67 and 71a-b). Some of the deep invaginations into the body appear in some of HOLM's plates (WILLS 1965: pl. 4 fig. 5) more like flattened canals rather than elongate clefts. It is important to notice that the polygonal surface with the rosettes continues into the narrow clefts (text-fig. 71). The invaginations lead into masses of spongy chitin, structures which according to WILLS also occur above the ridges (indicated

---

[2]) In a recent paper GOULD & RAYMOND (ANDREWS et al. 1974: 82) are inclined to regard *Baltoeurypterus tetragonophthalmus* (FISCHER 1839) merely as a subspecies of *Eurypterus remipes* (DEKAY 1825). The differences in the paddle are supposed to be too small to warrant a generic separation. In their careful statistical treatment of the eurypterids the authors have, however, not statistically examined the variation between the different segments of the distal portion of the last leg (the portion usually called the paddle). Other morphological characters which seem to warrant the establishment of the genus *Baltoeurypterus* will be described by KJELLESVIG-WAERING in a forthcoming paper.

in his reconstruction reproduced in text-fig. 65). The spongy masses are penetrated by numerous canals and cavities evidently with very thin-skinned cell-walls (WILLS 1965: 128).

According to WILLS' interpretation of the structures, the gill-tract was situated below a blood-sinus and served as a gill. Deoxygenated blood from the body was carried to the capillary sized cells of the spongy mass. Gas exchange took place through the thin walls of the cells. Oxygenated water was introduced into the deep invaginations between the corrugations on each ridge. The down-hanging ridge-folds of the body-wall and extra folds (text-fig. 65) might according to WILLS indicate pulsatory movements of the ventral plates ("Blatt-füße") and the gill-pouch. The oxygenated blood was eventually collected into one or two "trunk-veins" passing towards the lateral point of the gill-tract.

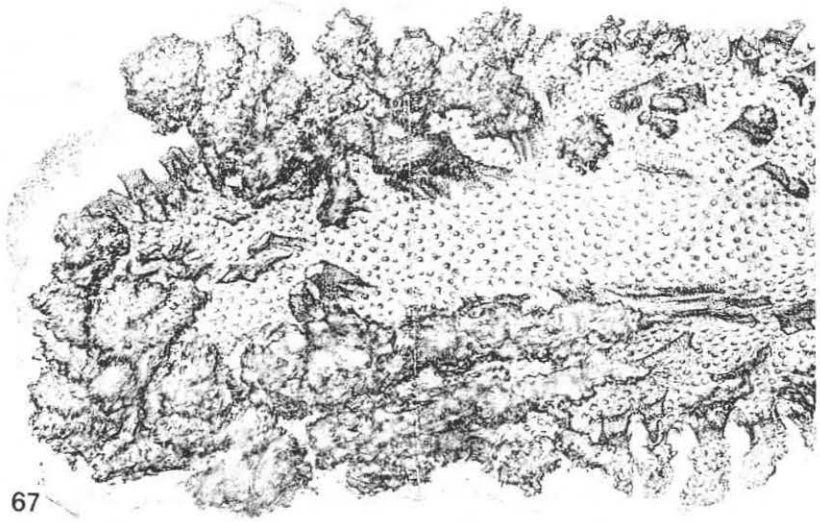
WILLS (1965: 122) compares the respiratory structures in *Baltoeurypterus* with those in *Limulus* only. He finds "that no close comparison can be drawn between the ridged and spinule-covered gill-tract of *Eurypterus* [*Baltoeurypterus*], which is a modification of the ventral body-wall, and the gill-book of the adult *Limulus*". On the other hand he assumes with regard to the respiratory structures that it is easy "to envisage the course of evolution, from their position in the ventral body-wall to one on the proximal part of the inside of the gill-appendage". He further states that the large ridges on the gill-tract of *Baltoeurypterus* "can be thought of as an outfold of the skin not differing essentially from one of the elongate evaginations seen on the embryonic *Limulus*" (comp. text-fig. 59). In the Xiphosura transverse lamellae arise as outpouchings of the ectoderm of the posterior face of each limb, the first lamella being the most distal (ANDERSON 1973: 439).

In my opinion the respiratory structures may successfully be compared also with those in other arthropods than the Xiphosura. In interpreting the respiratory structures in *Baltoeurypterus* we want primarily to know the function of the organs, not necessarily the real homologies. It is well known that among the Arthropda very similar respiratory organs may develop in very different groups, e. g., the development of similar tracheae in Onychophora, Arachnida, Myriapoda and Insecta.

I agree with WILLS that a gaseous exchange took place through the thin walls of the cells in the spongy mass penetrated by fine canals apparently opening on the surface of the deep invaginations of the gill-tract. However, it seems likely to assume that in a comparatively big arthropod like *Baltoeurypterus* the whole surface of the gill-tract would have served as a respiratory organ, not only the areas with the spongy masses above. Water entering and passing out through the narrow and deep furrows or canals between the ridges could hardly be sufficient to manage a satisfactory gaseous exchange necessary for the animal.

As mentioned by WILLS the cone-shaped pustules or spinules all over the surface of the gill-tract evidently serve to enlarge the surface. For comparison it might be mentioned that in the decapod crustacean *Birgus latro* (the "palm thief") the surface of the branchial chamber has grape-like ramified pustules enlarging the surface. Blood-lacunae extend into these pustules (KÄSTNER 1959: 863), and the same was probably the case in the fossil form. We know from

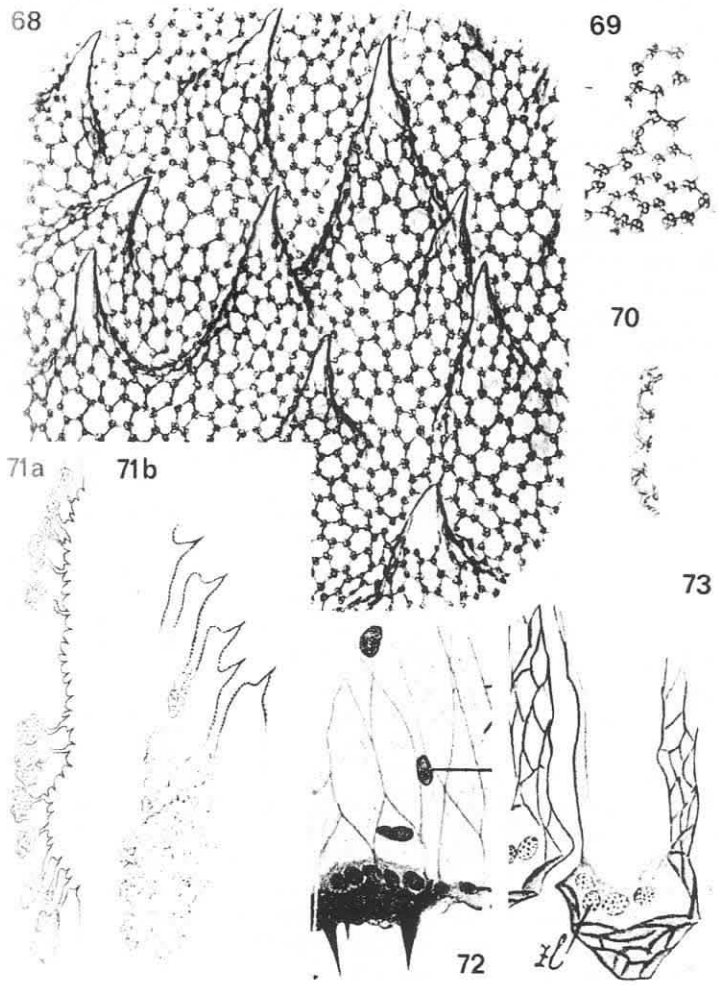
66



67

Text-figs. 66-67. Respiratory organs in Eurypterida. *Baltoeurypterus tetragonophthalmus* (FISCHER 1839). (After WILLS 1965.) — 66: Details of gill-tract with ridges (dark) and valleys (light). — 67: Retouched photograph of gill-tract showing in dorsal view the bulbous terminal expansions at the inner ends of the invaginations indicated in the reconstructed cross-section in text-fig. 65. The terminal bulbous portions of the invaginations have a spongy appearance resembling pseudotracheae of isopods (comp. text-fig. 80).

other arthropods that gas exchange may take place through thin chitinous membranes. In certain Recent scorpions such as the Buthidae, the thin membranes of the book-lung lamellae which are kept wet, are supported by chitinous bars or ribs forming a reticulate pattern (PAVLOVSKI 1926: 136). This pattern (text-figs. 72-73) resembles the structures in eurypterids. The polygonal areas of the gill tract in *Baltoeurypterus* were probably covered by a similar very



Text- figs. 68-71. Respiratory organs in Eurypterida. *Baltoeurypterus tetragonophthalmus* (FISCHER 1839). (Text-figs. 68-70 after WILLS 1965.) — 68: Details of gill-tract. Reconstruction of spinules with polygonal pattern of their chitinous ribs or bars with "rosettes" where the ribs meet. — 69-70: Reconstructions of ribs and "rosettes" in ventral and lateral view. — 71: Reconstruction of invaginations between spinules.

Text-figs. 72-73. Respiratory organs in Scorpionida. Chitinous ribs on lamellae of book-lungs (after PAVLOVSKI 1926).
72. *Anomalobuthus rickmersi* KRAEPELIN 1905.
73. *Odonotarus dentatus* KARSCH 1879.

thin chitinous cuticula, and this fragile structure was supported by the surrounding bars or ribs. The cone-shaped spine on the top protected the whole structure (text-fig. 68).

Since the eurypterids were mainly aquatic forms *a gaseous exchange from water to blood and vice versa probably took place through the thin membranes strechted out between the bars round the polygonal areas*. If the polygonal surfaces of the gill-tract did not serve as gills it is difficult to understand the function of these complicate structures.

The light portions above the pustules or spinules, particularly those above the "valleys" (WILLS 1965: pl. 4 fig. 7), were probably parts of a common blood sinus.

The problem remains how to explain the narrow clefts or canals leading into the spongy masses. One has to remember, as pointed out by UNWIN (1932: 54) that air can gain access more easily than water through narrow passages, clefts or canals. Among terrestrial isopods the passage of the air into the pseudotracheae is performed by pressure caused by up and down movements of the abdomen. It is possible that movements of the ventral plates, and a flection of the mesosoma in *Baltoeurypterus* to some extent, might have facilitated a transport through the narrow passages. Dr. WATERSTON has pointed out to me that he agrees with WILLS in his view that it is likely that the gills were quite three-dimensional and when full of blood in the living animal might well have had a cushion shape, and he further mentions that in that case the structures we see are probably crumpled and collapsed; we probably almost always are looking at exuviae. Even a more convex surface of the gill-tract would in my opinion hardly be sufficient to obtain big enough openings for an easy water passage. A slight rhythmic widening and concentration of the narrow passages might possibly have been accomplished by an increase and decrease of the blood-content of the blood-sinus. However, in spite of the possibilities mentioned it seems difficult to assume that enough water could pass easily through the narrow passages.

Strangely enough the invaginations and spongy masses in *Baltoeurypterus* show considerable resemblance to the pseudotracheae in terrestrial isopods (p. 146; text-figs. 80a-b). Although the detailed structures of the spongy masses are unknown, fine canals through the masses have been observed. In terrestrial isopods like *Porcellio* both sides of the entrance into the pseudotrachea are coated with flat and short polygonal tubercles (p. 147; text-figs. 80b-c). According to UNWIN (1932) the flat and short polygonal tubercles are able to retain the air in the furrows between them and, thus, being able to prevent the surface from becoming wet. A wet surface is apt to clog the entrance into the fine canals of the pseudotracheae. Similar structures occur in insects, among them in aquatic forms where they prevent water from entering into the spiracles. In *Baltoeurypterus* the polygons with the short-stalked rosettes occur all over the gill-tract including the narrow entrances into the spongy masses. In the latter places it is possible that the rosettes could retain some air and eliminate clogging.

As mentioned above a further correspondence in structure between eurypterids and terrestrial isopods in particular is demonstrated in the ramification of the blood-vessels (text-figs. 64, 66 and 81). As in *Ligia* the marginal vessels in *Baltoeurypterus* would carry blood from the body of the gill (afferent vessels), and the main trunk oxygenated blood back to the body (efferent vessels).

The present assessment of the structures in *Baltoeurypterus* leads us to the unexpected and at first sight unlikely assumption that *the gill-tract might have acted both as gill and pseudotrachea.*

This would imply that the eurypterid *Baltoeurypterus tetragonophthalmus* was amphibious in its mode of life. The paddles of many eurypterids indicate swimming abilities and a common occurrence of eurypterids with aquatic forms indicates that the main habitat of this eurypterid was aquatic. It may be mentioned, however, that a recent study of a track of the Silurian eurypterid *Mixopterus* (HANKEN & STØRMER 1975) shows that at least this eurypterid was able to use its paddles as walking or crawling legs.

If the present interpretation is correct, several eurypterids at least might have been able to leave the water and stay on land for shorter or longer periods. They may have been able to move or at least stay above the supralitoral zone and, thus, being more terrestrial in their habits than the Recent *Limulus*. Eurypterids without paddles, such as members of the superfamilies Drepanopteroidea, Stylonuroidea and Mycteropoidea, probably were more fitted for walking on land. The Recent decapod *Birgus latro*, the "palm thief", which may obtain a length up to 32 cm, might be compared with the good-sized eurypterids.

Dr. WATERSTON has pointed out to me, and I agree with him, that it seems very unlikely that the big pterygotids such as *Pterygotus anglicus* were able to walk on land. These eurypterids were evidently good swimmers, and the very slender prosomal legs were hardly fit for carrying the large body in a non-aquatic environment. However, the presence of some kind of lungs might still have been useful in these "fish-like" forms. As shown in previous papers the eurypterids to a large extent may have lived in estuaries and lagoons which occasionally, particularily in tropical arid areas, may dry up leaving the animals stuck in the mud. During Lower Devonian time the crossopterygians and lungfishes needed their lungs to survive in the drying up streams with water present only in stagnant pools. If we had not had the acanthopterygian *Polypterus* and the living lungfishes, it might have been very difficult to assume that the air-bladder served as lungs in the Old Red fishes. The Recent *Polypterus* lives in tropical regions in which there are alternating periods of rain and draught, conditions similar to those along and on the Old Red continent. Pterygotids living partly in estuaries and lagoons might very well have needed some kind of pseudotracheae to survive during dry seasons. However, like the fishes mentioned, these eurypterids were hardly fit for walking on land.

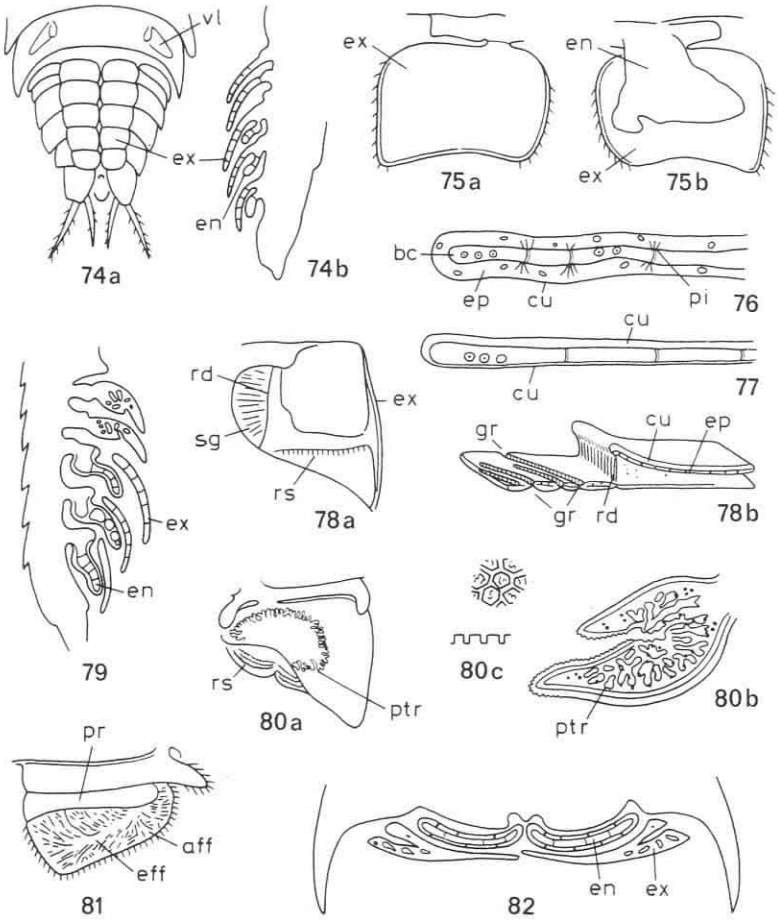
The partial terrestrial mode of life of eurypterids is suggested in the diagram (text-fig. 107).

Crustacea

Terrestrial representatives are found among the Isopoda, Amphipoda and Decapoda. These forms are generally very susceptible to dry air and therefore prefer a moist environment such as wet plant debris, protected niches beneath stones etc. The cryptic faunas of the rain forests include many of the terrestrial or partly terrestrial forms (LAWRENCE 1953). Since the diffusion constant in the air (dry chitin) is only one-thirtieth of that in water (EDNY 1960: 375) the typical gill of marine animals is not very useful in the air.

However, the gills of terrestrial crustaceans are strangely enough very little different from those of crustaceans living in water. The simple reason is that the terrestrial forms produce an artificial aquatic environment for the gills by covering their surface by a film of water or by liquids produced by special glands.

Terrestrial Amphipoda, the "leaf-mould amphipods" or "landhoppers", are found more particularly in the Southern Hemisphere (HURLEY 1968). Many species are just as independent of the water as are the woodlice and myriapods, but they prefer the leaf-mould or cryptozoic zone which is primarily a humid, insulated, temperated and food-filled habitat. Due to the high relative humidity the respiratory organs are little modified; the only necessary feature being a considerable development of the gill surface. According to HURLEY (1968: 329) the terrestrial forms probably evolved from supralitoral species invading the



land through the algal debris zone. In the Pacific the forests frequently extend right to the waters edge, and algae and litter are contiguous, conditions which may have existed in Lower Devonian time (see p. 133).

The terrestrial Decapoda breathe both by gills, well protected in the branchial chamber, and by the vascularized lining of this chamber (the "lung" of the land crab). The terrestrial crabs carry air only in their branchial chambers and this air has to be renewed in order to increase the O_2-content. The number of gills is reduced, but "the branchial epithelium remains moist because the branchiostegites fit snugly against the body" (BLISS 1968: 310). With regard to the resistance against desiccation the terrestrial decapods are more advanced than are both the amphipods and isopods, but unlike these they have to return to the lakes and rivers or to the sea to spawn.

In contrast to the decapods and amphipods the Isopoda have developed several different ways of adapting their respiratory organs to an amphibious or terrestrial mode of life. The various structures developed may prove important to the interpretation of fossil arthropods, e. g. the eurypterids, and are therefore dealt with in more detail below.

◀

Text-figs. 74-82. Respiratory structures in terrestrial isopods (after UNWIN 1932; text-figs. 78a-b modified by KÄSTNER 1959). — All not drawn to scale. — aff = afferent vessels; bc = blood cavity; cu = cuticula; eff = effluent vessels; en = endopod; ep = epithelial layer; ex = exopod; gr = groove; pi = pillar; pr = protopod; ptr = pseudotracheae; rd = longitudinal ridge or edge; rs = row of setae; sg = sigmoid rim; wl = walking leg.

74-77. *Trichoniscus pusillus* BRANDT 1833. — 74: Abdomen. a) Ventral view; × 24. b) Longitudinal section. — 75: One of the three last pairs of abdominal appendages (pleopods). Exopod well protected by endopod. a) Ventral view. b) Dorsal view. — 76: Cross-section of exopod. Cuticula thin, epithelial layer relatively thick; pillars penetrating blood cavity, support the structures; about × 350. — 77: Transverse section of exopod. Epithelial layer on ventral wall very thin.

78. *Oniscus asellus* LINNAEUS 1758. — a) Dorsal view of fifth abdominal appendage; sigmoid rim with radiating transverse grooves bordered medially by longitudinal ridge or edge; a row of setae transverse the dorsal surface of endopodite. — b) Diagrammatic section across ridge and sigmoid area with grooves.

79. *Porcellionides pruinosus* (BRANDT 1833). — Longitudinal section of abdomen showing pseudotracheae on the dorsal (posterior) surface of the two first appendages; on the three last appendages spongy endopods are present.

80. *Porcellio scaber* LATREILLE 1804. — a) Exopod of second appendage (pleopod) in dorsal view; entrance to pseudotracheae protected by rows of setae. — b) Section of bulbous anterior exopod with pseudotracheae; surface of distal portion of entrance into pseudotrachea with flattened hexagonal tubercles. — c) Surface and cross-section of tubercles at the entrance into pseudotrachea.

81. *Ligia oceanica* (FABRICIUS 1798). — Blood vessels of endopod; afferent vessels unite into a common effluent vessel; the protopod covers the endopod.

82. *Cylisticus convexus* (DE GEER 1778). — Cross-section showing endopods well protected in ventral body cavity by the plate-shaped exopods with pseudotracheae.

The classical studies of UNWIN (1932) demonstrate various kinds of modifications in the pleopods of terrestrial isopods (text-figs. 74-82). The short and flat pleopods consist of a very short protopodite to which an exopodite is attached (text-figs. 75a-b). The lower (ventral) exopodite covers the endopodite above situated just below the body wall. The pleopods overlap each other backwards (text-figs. 74a-b and 79). Both the exo- and endopodites take normally part in respiration.

A cross-section of the leaf-like appendages shows a double wall consisting of an inner epithelium and an outer chitinous cuticula (text-figs. 76-77). The two walls are supported and held in place by vertical pillars.

The blood circulation is well demonstrated in *Ligia* (text-fig. 81). The blood enters (afferent vessels) at the articulation of the protopodite and exopodite, and passes along the margin of the exopodite with branches running inward close to the ventral surface where only a thin wall separates the vessels from the air outside.

The endopodites of the first and second pleopods are usually completely reduced in terrestrial forms (text-fig. 74b) (in *Ligia* a rudimentary second endopodite is present). Four main adaptive modifications of respiratory organs in terrestrial isopods are briefly described below (based on UNWIN 1932).

(1) In *Trichoniscus pusillus* the endopodite with its moist surface functions as a gill and is kept wet by the underlying exopodite serving as a protecting operculum (text-figs. 74a, 79 and 82). In order to be able to close the branchial chamber as much as possible the lateral portions of the posterior abdominal segments in *Cylisticus convexus* are bent down to form a shallow cup-like cavity (text-fig. 82). The structures are similar to those in *Limulus* (text-fig. 60) and may, as suggested above, be called the *Limulus*-method of protecting the gills from desiccation. The endopodite serving as a gill has a thin cuticula and a thick epithelium (text-fig. 76).

(2) A first adaptation to air-breathing, i. e., to have a gas exchange directly from the air to blood, is also demonstrated in *Trichoniscus pusillus*. A cross-section of the exopodite (text-fig. 77) shows how both the cuticula and epithelium of the ventral wall are very thin allowing the oxygen to get in close contact with the blood sinus above. On the other hand the dorsal wall of the exopodite has a very thick cuticula strengthening the leaf-like appendage which also serves as an operculum.

(3) A peculiar development of the exopodite is found in the woodlouse *Oniscus asellus* (text-figs. 78a-b). The dorsal surface has a lateral sigmoid segment very different from the rest of the appendage. The median portion of the appendage is much thicker than the lateral portion and is bordered laterally by a ridge with a steep lateral wall. The sigmoid segments have a corrugated surface with a silvery appearance due to air imprisoned in the furrows on the corrugated surface. The thin cuticula facilitates a gaseous exchange from the air, and the epithelial layer is also much reduced. Together with this organ of respiration *Oniscus* has gills (endopodites) which are useful under damp conditions.

(4) A further and final step towards the formation of lung-like structures is demonstrated in *Porcellionides pruinosus* and *Porcellio scaber* (text-figs. 79, 80a-c). In several terrestrial genera the main respiration is performed by the

exopodites of the two first abdominal appendages (text-fig. 79). The thick exopodites are penetrated by a bundle of fine canals uniting into a common broad canal or cleft opening on the dorsal surface. The air-tree or pseudotrachea serves as a lung. The thin lining of the fine canals brings the pseudotrachea in close contact with the blood of the blood-sinus. The cleft or major canal leading into the pseudotrachea has the chitinous cuticula divided into hexagonal areas separated by furrows (text-fig. 80c). The flat-ended processes have a maze-like arrangement of ridges and are provided with hairs. As in aquatic insects the furrows between the hexagonal areas retain air and thus prevent the cuticula from becoming wet, a condition which might cause a clogging of the finer canals. Renewal of the air in the pseudotrachea is obtained by pressure on the exopods caused by flexions of the abdomen. — The endopodites and the dorsal wall of the three posterior exopodites (text-fig. 79) also serve as gills in this group of terrestrial isopods. The thick wall of spongy protoplasm in the endopodites is a most efficient wall for respiratory exchange (Unwin 1932: 93). The gills have to be coated by a film of water, and new oxygen is supplied by movements of the appendage.

Conclusions.

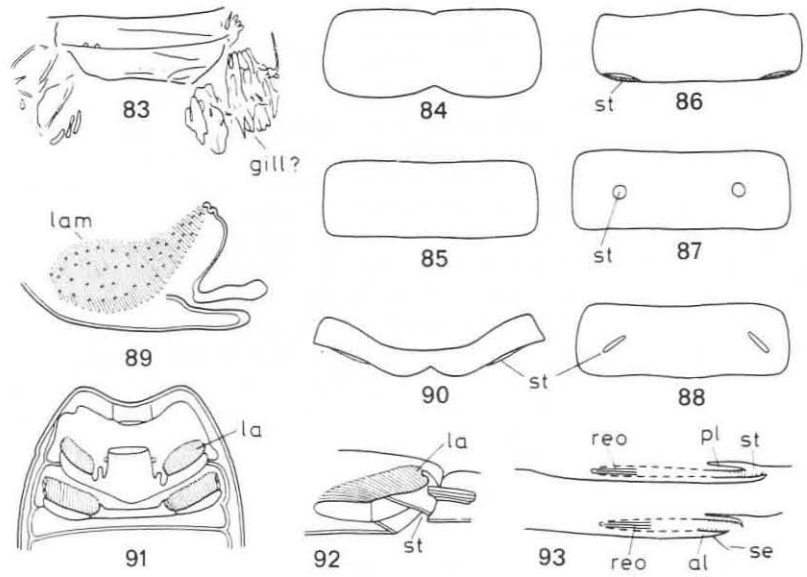
The adaptation to terrestrial life in Isopoda has developed along two main lines. Either the aquatic gills are maintained and kept wet, or the uptake of oxygen takes place directly from the air through the membranes either on the outer surface or in well protected invaginations (pseudotracheae). Although the gills and tracheal structures are limited to a few appendages, many isopods are fitted to spend all their life on land.

Arachnida.

Members of this group are often regarded as primarily terrestrial forms. The fossil record, however, indicates the presence of gills in certain Palaeozoic forms. It seems probable that the Recent terrestrial groups (or common ancestors to some of them) evolved from aquatic forms. A discussion of an aquatic origin of the scorpions is given in Part 1 (Størmer 1970: 349).

Recent arachnids have three kinds of respiratory organs: the book-lungs, the tracheae and the ventral or eversible sacs. The organs are primarily connected with the basal portion of the abdominal appendages.

As mentioned above (p. 137) the ventral abdominal plates of most Palaeozoic scorpions (text-figs. 84-85) are very similar to and apparently homologous with the plate-shaped appendages in eurypterids (text-fig. 63), which again are regarded as homologous with the abdominal appendages of *Limulus* (text-fig. 60; Størmer 1963: 110). The plates of the scorpions mentioned were probably attached to the body wall at the front only. In his excellent study of Triassic scorpions Wills (1946) describes elliptical openings along the posterolateral borders of the ventral plates in *Mesophonus* (text-figs. 86 and 93). These stigmata with thorns along the margins have a terminal or slightly dorsal position. According to Wills both the dorsal (posterior) or ventral (anterior) lips bordering the stigmata belong to the posterior doublure of the plate. Lateral



Text-figs. 83-93. Respiratory structures in Arachnida. — Not drawn to scale. — al = anterior lip; lam = lamellae between cavities; pl = posterior lip; reo = respiratory organ; st = stigma.

83. Scorpionida: *Waeringoscorpio heftert* STORMER 1970. Ventral plates with presumed ribbon-shaped gills. (After STORMER 1970.) — Lower Devonian; W. Germany.
84. *Eobuthus* FRITSCH 1904. Diagrammatic. Lobostern ventral plate. — Carboniferous. — Based on *E. holti* POCOCK 1911. Upper Carboniferous; Rochdale, England.
85. *Proscorpius* WHITEFIELD 1885. Diagrammatic. (After KJELLESVIG-WAERING 1961.) "Orthostern" ventral plate. — Silurian; New York.
86. *Mesophonus bromsgrowiensis* WILLS 1910. Ventral plate with posterolateral openings. (After WILLS 1946; comp. text-fig. 93.) — Triassic; Bromsgrowe, England.
87. *Palaeopisthocanthus schucherti* PETRUNKEVITCH 1913. Ventral plate with circular stigmata. (After VOGEL & DOURDON 1966.) — Carboniferous; Mazon Creek, Ill., USA.
88. *Pandinus* THORELL 1876. Diagrammatic. Ventral plate with stigmata developed as slits. — Recent; Africa.
89. Uropygida: *Thelyphonus* LATREILLE 1804. (From BÖRNER 1904.) Section of book-lung. (After MILLOT 1949.) — Recent; Asia.
90. Amblypygida: *Damon medius* (HERBST 1897). Ventral plate with posterior openings leading into book-lungs. (From KÄSTNER 1932 after BÖRNER 1902.) — Recent; Africa.
91. Uropygida: *Thelyphonus* LATREILLE 1804. Book-lungs of the two first abdominal somites. (After KÄSTNER 1932.) — Recent; Asia, Africa.
92. Arachnida: Diagram of book-lung with opening (stigma) along the posterior border of ventral plate or sternite. (From KÄSTNER 1932.) — Recent.
93. Scorpionida: *Mesophonus bromsgrowiensis* WILLS 1910. Two longitudinal sections showing posterior openings leading into book-lungs (?). (After WILLS 1946; comp. text-fig. 86.) — Triassic; Bromsgrowe, England.

doublures of the ventral plates do not seem to be present and it is therefore probable that the plates were also attached to the body wall along the lateral borders, leaving only a small free portion corresponding to the width of the posterior doublure.

As mentioned by WILLS (1946: 33) and STØRMER (1963: 110) *Mesophonus* probably forms a transition between the early Palaeozoic scorpions, in which the abdominal plates probably were attached in front only, and the Recent forms in which the ventral plates are attached all around as ordinary sternites.

In Recent scorpions the openings or stigmata occur as slits in the middle of the ventral plates (text-fig. 88). However, the ontogeny of scorpions shows

94

Text-figs. 94-99. Respiratory structures in Araneida: Embryological development of book-lungs in *Agelena labyrinthica* LINNAEUS 1758. (After KAUTSCH 1910; not figured to scale.) — Recent; Europe.

94. Four buds represent a primordium of the second to fifth abdominal appendages. At the posterior surface of the first primordium 3-4 transverse lines occur. These faint furrows develop into book-lungs as demonstrated in the following sections.

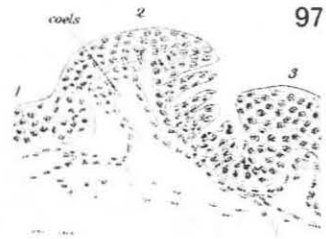
95-97. Longitudinal sections showing how the furrows develop on the posterior side of primordium.

98-99. The lamellae with the deep furrows between sink into the body forming the book-lung. The opening leading into the book-lung is not cut by the section.

95

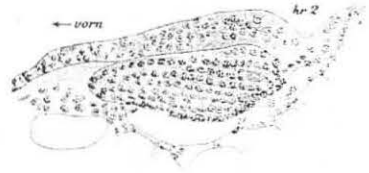
96

97



98

99



that the openings originate at the posterior border of the segments, and migrate forward during later development to their final position in the adults (KÄSTNER 1940a: 113). A migration of an opening into a solid sclerite is not unusual in arthropods. In myriapods the apertures for the antennae thus migrate into the solid head capsule. It is significant that in several arachnids such as the Uropygi and Araneida the openings into the respiratory organs occur at the posterior border (text-figs. 89-90, 92 and 99).

The earliest known scorpion with stigmata has been described by VOGEL & DURDON (1966) from the Carboniferous. The stigmata are small and circular (text-fig. 87) as in Recent Chactidae (KÄSTNER 1940b: 186).

In Recent arachnids the stigmata or posterior openings in Scorpionida, Uropygi, Amblipygi and Araneae lead into the book-lungs. The embryological development of the book-lungs is well demonstrated by KAUTSCH (1910) in the spider *Agelena labyrinthica* (text-figs. 94-99). The bud representing the primordium of the first of four abdominal limbs, has 3-4 transverse grooves near its hind base (text-fig. 94). The position of these grooves corresponds to the location of the embryonic gill-lamellae in *Limulus* (text-fig. 59). The microtome sections (text-figs. 95-99) clearly show how the grooves extend inwards, and how the intervening ridges develop into lamellae, the surfaces of which form the respiratory walls of the later book-lungs. At the same time the posterior position of the primordium sinks into the body wall leaving an opening which eventually becomes the outer entrance into the book-lung. Because of the close correspondence in the embryology and general structures of the book-lungs of the Arachnida and the book-gills of the Xiphosura there seems to be no reason to doubt that these structures are homologus as emphasized by LANKESTER and KINGSLEY (see ANDERSON 1973: 439).

Tracheae occur in most arachnids, in the primitive Onychophora, and in myriapods and insects. The tracheae are of two kinds, those which are homologous with the book-lungs and those which are secondary formations (KÄSTNER 1940a: 114). In the first case the tubules or strongly ramified structures are regarded as derivations from the anterooms of the book-lungs, the lateral respiratory organs developing on the rear side of 8th and 9th primordium, as do the book-lungs. The median trachea on the 9th segment has a quite different origin. The prosomal stigmata are also secondary formations.

Ventral or eversible sacs, described below, occur in most Holopeltida and in the Palpigradi.

The fragile respiratory organs in arachnids are very rarely preserved in fossil specimens. Fossil remains, evidently representing book-lungs with stigmata, have been described by CLARIDGE & LYON (1961) from the probably Lower Devonian Rhynie Chert in Scotland. The authors have kindly permitted me to reproduce some of their original photographs (pls. 9-10). The presumed book-lungs are referred to terrestrial arachnids, probably of the family Palaeocharinidae of the order Trigonotarbida (HIRST 1923) which also occur in the Nellenköpfchen-Schichten of Alken (STØRMER 1970).

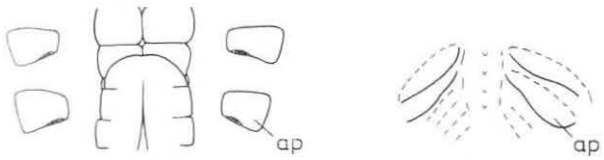
The excellently well preserved book-lungs from Rhynie are almost identical with those in Recent arachnids, e. g., in Uropygida and Araneida (text-figs. 89-91). It is interesting to ascertain that already in Devonian forms only the two anterior abdominal segments had book-lungs (pl. 9 fig. 2). This fact con-

firms the general impression of the great conservatism in arachnid structures. As in Recent forms the stigmata leading into the book-lungs evidently were situated at the posterior border of the ventral plates.

Waeringoscorpio from Alken shows tufts of probable gills extending from the postero-lateral corners of posterior abdominal segments (text-fig. 83; STØRMER 1970). The structures have a certain resemblance to the tracheae in the Ricinulei (MILLOT 1949: 313, text-fig. 90). Because of their delicate nature (I am afraid they will fade away in the specimen within a few years), I was inclined to assume that they could be withdrawn into the cavity above the ventral plates, but as pointed out to me by Professor WHITTINGTON this may not necessarily have been the case.

In *Mesophonus* WILLS (1946: 30) has found traces of respiratory organs appearing as dark blotches above the ventral plates. "Under a high power the blotches appear reticulate, and in some forms the minute spinous ends of the numerous lamellae are clearly to be seen" (text-fig. 93). He adds, however, that the reticulation might be due to accidents in preservation. Mr. KJELLESVIG-WAERING has suggested to me the possible resemblance to the reticulate surface with spinules in eurypterids (see p. 138). The similarities may either be homologous or analogous structures, but in any case the chitinous ribs in both forms seem to serve as supports of the thin membranes.

Returning to the ventral plates in arachnids I have postulated (STØRMER 1963) that they may be regarded as modified appendages rather than primary sternites. In general I do not regard ventral plates of the body wall as primary sternal structures. They develop when there is need for protection, articulation of appendages or attachment of muscles. It is significant that in chelicerates with large prosomal coxae the sternites are more or less reduced. The ventral plates with book-lungs above, may either be modified appendages or true sternites. If we deduce from the ventral plates in Xiphosura-Eurypterida-primitive scorpions, the "sternites" might be interpreted as modified plate-shaped appendages fused along their borders to the body wall. If on the other



100 101

Text-figs. 100-101. Development of the ventral abdominal plates in Scorpionida and Xiphosura. — Not drawn to scale. — ap = abdominal appendages.

100. *Euscorpius carpathicus* LINNAEUS 1758. Embryological stage showing flat primordia of abdominal appendages. The book-lungs appear as folds at the steep posterior border of the flat primordia. — Recent; Europe.

101. *Tachypleus gigas* (MÜLLER 1785) [= *Limulus moluccanus* LATREILLE 1802]. Early stage in the development of the abdominal appendages. (From IVANOV 1933, pars.) — Recent; SE. Asia.

hand a comparison is based on the book-lungs as the only modified appendages, the interpretation may be different. The embryology of the Xiphosura indicates very broad appendages (text-fig. 101). In the Scorpionida each primordium is also rather broad with a steep hind margin where the book-gills develop and become invaginated (text-fig. 100). It is possible that the anterior portion of the primordium merges with the surrounding surface forming a sternite. We would then have a composite structure, a sternite in which the rear part developed from the anterior portion of an appendage.

The fossil record indicates that the terrestrial arachnids, at least the scorpions, evolved from aquatic forms breathing with gills, either bundles of ribbon-like gills, or book-gills. The book-gills were replaced by book-lungs, and additional respiratory organs in the form of tracheae were developed and might occur together with the book-lungs. According to LAWRENCE (1953: 139) the arachnids have a largely incomplete respiratory system, only the Solifugae being fully active thanks to a well developed tracheal system.

Myriapoda and Insecta.

All the living forms have a well developed tracheal system. Unfortunately the fossil record presents very little information of the respiratory organs in Palaeozoic myriapods. No details of ventral structures are demonstrated in the Siluro-Devonian forms described by PEACH (1883). Descriptions of ventral structures in Carboniferous myriapods by FRITSCH (1883-1901) need to be revised. The original material of FRITSCH is now being restudied by KRAUS (1974).

The ventral or coxal sacs might be regarded as primitive respiratory organs functioning as less efficient gills. However, together with tracheae, they would have been useful to arthropods living in a damp environment, particularly amphibious forms. HOFFMAN (1969: *R* 577) mentions that there is some reason to suspect that at least several species of the Palaeozoic Archipolypoda among the Myriapoda may have been aquatic or semiaquatic, and PETRUNKEVITCH (1955: 89) assumes that the extinct Architarbida might have used ventral sacs as organs of respiration. The possible presence of ventral sacs in Arthropleurida is discussed above. The respiratory function of the eversible sacs in onychophorans has, however, been doubted by ALEXANDER & EWER (1955). They conclude that the main function is that of water resorption.

The rather detailed record of the respiratory organs of fossil and Recent amphibious and terrestrial arthropods has been presented in order to facilitate the possible interpretation of present and future finds of fossil respiratory structures.

Modifications of morphological characters related to movement.

The change from an aquatic to a terrestrial mode of life implies an increase in weight on the appendages applied in walking. In small arthropods this additional weight is of minor importance and special adaptations are not significant. However, the load on the appendages increases rapidly with an

increasing body size. The largest, probably amphibious and terrestrial arthropods are known from the Carboniferous: *Arthropleura*, length up to 180 cm (?) (ROLFE 1969); *Cyrtoctenus*, 150 cm (?) (STØRMER & WATERSTON 1968); *Gigantoscorpio*, 52 cm (if we base the length on a foot evidently belonging to the species as pointed out to me by Mr. KJELLESVIG-WAERING) (STØRMER 1963); certain giant arthropods such as *Pterygotus*, at least 180 cm, and certain other eurypterids as well as the scorpion *Brontoscorpio* (KJELLESVIG-WAERING 1972) are known also from the Silurian and Devonian.

Since the tubular sclerites of the arthropod legs are very strong, the terrestrial adaptations are mainly restricted to the muscles which can not be directly observed by the palaeontologists. However, the structure of the distal portion of a leg might give some information regarding the habitat. POCOCK (1911: 306) suggested that in the Silurian scorpion *Palaeophonus* the sturdy legs terminating into a single spine might have been adapted to an aquatic life.

Because of the weight of the body on land, the larger forms would need an appreciable area of contact between the leg and the ground, if the number of legs were not too numerous and the animals did not crawl on their bellies. A "plantigrade" foot is found in terrestrial scorpions and also in *Limulus* (useful as pushers and when walking on a soft bottom or on the beach (STØRMER 1963: 90). A "digitigrade" foot is characteristic mainly of aquatic arthropods such as crustaceans, eurypterids and xiphosurans. Most arachnids have walking legs with blunt ends provided with two small spines.

However, one has to be very cautious in interpreting the functions of an arthropod leg merely from its general morphology in fossil specimens. The paddles or swimming legs in eurypterids are generally regarded as adapted for swimming, balancing (fins) and digging. However, a track of the eurypterid *Mixopterus* (HANKEN & STØRMER 1975) has shown that the paddles could be used in walking also.

The shape of the body in the fossil forms may to a certain degree indicate their mode of life, whether they were aquatic or terrestrial. The stream-lined body of the Hughmilleriidae and the "tail-fin" of the Pterygotoidea suggest very active and capable swimmers.

Modifications of sensory organs.

Finer anatomical details of sensory organs are usually not preserved in fossil forms. In certain cases, however, modification of sensory organs due to a transition from aquatic to terrestrial life are suggested.

In eurypterids the short and rigid tactile setae are well suited for resisting the water pressure when moving in water. Recent terrestrial scorpions have long and flexible setae or hairs attached to the bottom of a cup, the so called trichobotria, which serve as special tactile organs when moving in the air. These sensory hairs, situated on the pedipalps, register slight movements in the air and thus serve as some kind of a "radar". The well preserved *Gigantoscorpio willsi* from the Carboniferous lacks the trichobotria but has numerous "eurypterid" setae which suggest that this scorpion was mainly aquatic or at least amphibious (STØRMER 1963: 26, 96).

It is interesting to ascertain that both terrestrial and presumed aquatic scorpions have well developed combs or pectines evidently provided with different kinds of muscles. In aquatic scorpions the combs might to some extent have served as movable fins, and the thin-walled hollow peg organs on the teeth might have been able to register changes in pressure of the surrounding water. However, the function of the combs in Recent terrestrial forms is still uncertain. KÄSTNER (1940b: 149) observed how the combs went up and down when the scorpion passed over an uneven surface. This may suggest that the peg organs are able to register slight changes in the air pressure. Several other functions have also been suggested. I have not studied the literature on possible changes in sensory organs in crustaceans adapted to terrestrial life.

Development of preoral cavity.

The presence of a preoral cavity or chamber appears to be characteristic of true terrestrial arthropods. This structure is found in arachnids, myriapods and insects. The preoral cavity is a composite structure usually formed by the protruding head-shield, the upper lip (labrum), the lower lip (labium), one or two frontal sternites and the basal portions of the frontal appendages of the head. The cavity is open in front where the prey is held and chopped by the chelicers in the arachnids and by the mandibles in the myriapods and insects. The extraoral digestion is not complete; smaller pieces of food may reach the mouth and pass into the intestine. The development of a preoral cavity in the Arachnida, Myriapoda and Insecta is briefly described.

Arachnida.

KÄSTNER in particular (1925, 1940a, 1940b), has pointed out the presence of a preoral cavity in the arachnids (text-fig. 104). It is interesting to note that this structure appears to develop independently in the various orders, a feature demonstrating an adaptation to a common way of feeding: "Ein gemeinsamer Charakter zeigt sich endlich darin, daß bei den behandelten Gruppen ein Streben nach der Bildung eines präoralen Mundraumes mit Hilfe der Gliedmaßen vorhanden ist" (KÄSTNER 1925: 733). An early stage in the development of a preoral cavity is demonstrated in the primitive and very small Palpigradi (up to 1·5 mm in length without flagellum). Here the short and primitive cavity is bordered by the protruding prosomal exoskeleton, the basal sides of the chelicerae, the labrum and the labium ("hypostoma"), and the basal portions of the pedipalps (BÖRNER 1901). The embryonic development of the labrum is well demonstrated in *Thelyphonus* (Uropygi) (KÄSTNER 1949).

The embryological development of a preoral cavity in scorpions shows that the bottom or parts of the side of the cavity are formed by extensive coxal processes — the maxillary processes or "Laden".

The preoral structures in the Scorpionida are of particular interest since information on their development is provided by fossil species from the Silurian onwards in the Palaeozoic. The embryological development of the scorpion shows how the maxillary processes gradually develop and the sternite becomes reduced in connection with the formation of the preoral cavity. Mr. KJELLESVIG-

WAERING who is soon finishing a comprehensive monograph on Palaeozoic scorpions will be able to elucidate the gradual development of the maxillary lobes and reduction of sternae in different scorpionid families. The present material of *Waeringoscorpio hefteri* (see STØRMER 1970) demonstrates a primitive form in which the maxillary processes are not yet developed and a large composite sternum fills the space between the coxae. This species represents what we may call a "palpigrade" stage in the evolution of the Scorpionida. Other Palaeozoic scorpions, not necessarily in chronological order, illustrate further stages towards a well developed preoral cavity (STØRMER 1970: text-fig. 5). *From the early probably aquatic to the late terrestrial scorpions, we thus notice a gradual evolution which conforms with general embryological development of arachnids, and also with primitive and advanced stages demonstrated in the various groups of living arachnids*

Myriapoda.

A well developed preoral cavity is characteristic of the Symphyla, Chilopoda, Diplopoda and Pauropoda (text-fig. 105). As mentioned above (p. 103) TIEGS' (1940) important study of the embryology of the symphylid *Hanseniella* (text-figs. 26-30) shows how the oesophagal opening or stomodaeum appears in the earliest stages as a transverse slit on the ventral surface. Gradually the sternae behind the stomadaeum migrate into the slit and become covered in ventral view by the buds of the gnathal elements: the mandibles, the first maxillae and the second maxillae, the latter becoming fused forming a labium behind the opening leading into the developing preoral cavity. These are the first stages in the formation of the preoral cavity (text-figs. 26-30). Meanwhile the opening has migrated forwards. To begin with, the coxae have a transverse direction; later they become anterolaterally directed, and finally they reach a nearly longitudinal orientation towards the mouth in front.

Within the various myriapod groups the gnathal limbs form the sides and floor of the preoral cavity. In the Symphyla the basal plate of the two-jointed mandible is implanted on the side of the head. The roof of the cavity is formed by the epipharyngial surface, the floor covered by a gnathochilarium which possibly is a combination of a sternum and the maxillae.

Little is known of the gnathal structures in Palaeozoic myriapods. The present study of *Eoarthropleura* suggests certain ventral structures of the head. A small oblong plate (pl. 8 fig. 1; text-figs. 5, 23a-b) resembles the mandibles of the myriapods, and a cordate plate (pl. 8 fig. 2; text-figs. 15-17) is tentatively interpreted as a labrum and placed in front of the mouth in the reconstructions (text-figs. 24, 46). If this interpretation is correct the structure and position of the mouth region deviates considerably from Recent forms, but on the other hand it may correspond to the embryonic structures in primitive myriapods such as *Hanseniella* (text-figs. 26-29).

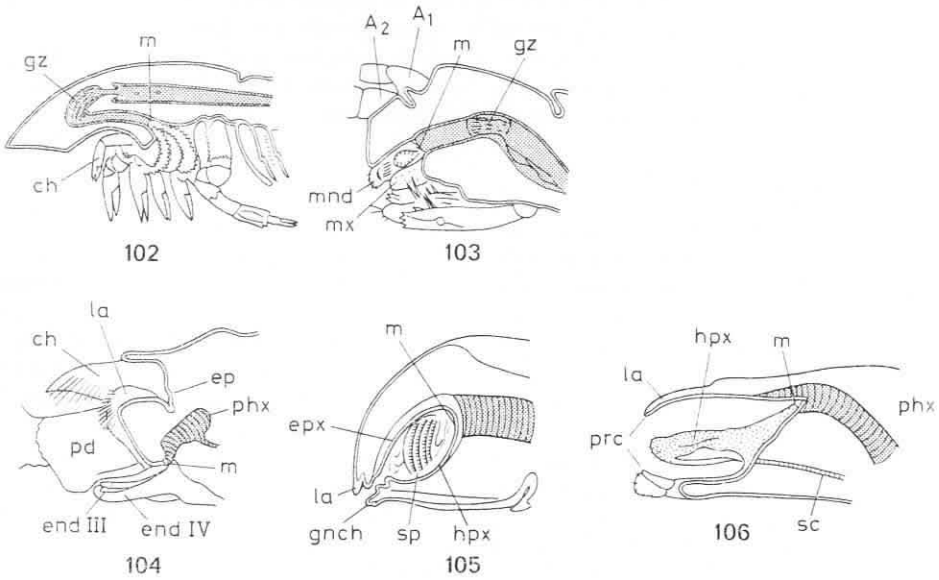
Insecta.

The preoral cavity in Insecta (text-fig. 10b) largely corresponds to that of the Myriapoda.

Function of preoral cavity.

The Arachnida have an external digestion. The prey which is caught and chopped by the pedipalps and chelicers, is brought into the preoral cavity where it is largely dissolved by enzymes from the midgut.

The feeding and digestion seem to be the same in the Myriapoda. KÄSTNER (1968: 380) describes how in a member of the Chilopoda "the maxillipeds cut up the internal organs, permitting deeper and deeper penetration by the



Text-figs. 102-106. Absence and presence of a preoral cavity in arthropods. The aquatic xiphosuran (102) and isopod (103) have no preoral cavity developed (a slight indication may perhaps be seen in *Idothea*). A preoral cavity is characteristic of the terrestrial Arachnida (104), Myriapoda (105) and Insecta (Hexapoda) (106). — Not drawn to scale. — A_1, A_2 = first and second antenna; ch = chelicera; end = third and fourth endites; ep = epistoma; epx = epipharynx; gnch = gnathochilarium; gz = gizzard; hpx = hypopharynx; la = labrum; m = mouth; mnd = mandible; mx = maxilla; pd = protopod; phx = pharynx; prc = preoral cavity; sc = salivary duct; sp = gnathal row of spines in preoral cavity.

102. Xiphosura: *Limulus polyphemus* (LINNAEUS 1758). (From KÄSTNER 1959, after PATTEN & REDENBAUGH 1899.) — Recent; Atlantic coast of N. America.

103. Crustacea, Isopoda: *Idothea baltica* PALLAS 1772. (From KÄSTNER 1959, after NAYLOV 1955.) — Recent; Europe.

104. Arachnida, Scorpionida: *Centruroides* EHRENBERG 1829. (Simplified from SNODGRASS 1952.) — Recent; N. and S. America.

105. Myriapoda, Diplopoda: *Cylindroiulus teutonicus* (POCOCK 1900). (Simplified from FELTER 1961.) — Recent; Europe.

106. Insecta: *Periplaneta americana* LINNAEUS 1758. (Simplified from SNODGRASS 1952.) — Recent; America.

predator. At the same time one can see currents of fat droplets alternately flowing toward the mouth and away, suggesting the expulsion of enzymes. Absence of particles in the guts of 750 digested animals, and the relatively small mandibles provide evidence that digestion takes place outside the digestive system."

The aquatic Merostomata and Crustacea have no distinct preoral cavity (text-figs. 102-103). In *Limulus* the prey is chopped and chewed by the chelicerae and the coxae of the prosomal appendages, and afterwards led into the narrow cylindrical oesophagus and further into the gizzard.

Among the Crustacea the isopods (text-fig. 103) have a compact head resembling that of insects. The epistome (above the labrum) is, according to SNODGRASS (1952: 181), "an exact replica of the clypeus of an insect, on its basal angles are the articulations of the mandibles". As in *Limulus* the tube-shaped oesophagus leads into the gizzard, but an indication of the preoral cavity might perhaps be seen in the space bordered by a protruding upper lip, the inner (median) side of the mandibles and the more horizontal maxilla forming some kind of a floor. *Idotea* (text-fig. 103) shows these features.

We have seen how a preoral cavity is characteristic of true terrestrial arthropods. A tendency towards the development of a preoral cavity is traced in Recent primitive arachnids, and a similar trend is demonstrated in the Palaeozoic scorpions, a development which seems to coincide with a transition from an aquatic to terrestrial mode of life. In the myriapods also the structures in *Eoarthropleura* and the embryology of the Symphyla might suggest development from ancestors which probably were aquatic and did not yet have a preoral cavity. Evidently it was important for terrestrial arthropods not living in a damp environment, to develop a cavity in front of the mouth which was able to maintain the liquid environment necessary for the transport of the enzymes.

It seems probable that the formation of a preoral cavity in the Arthropoda was of decisive importance in completing the adaptation to terrestrial life.

It is interesting to compare the invasion of the land by arthropods with the somewhat later invasion by the vertebrates. The successful conquest of the land by the descendants of crossopterygian fishes (*Ichthyostega*) initiated the great development of the amphibians and the succeeding terrestrial tetrapods.

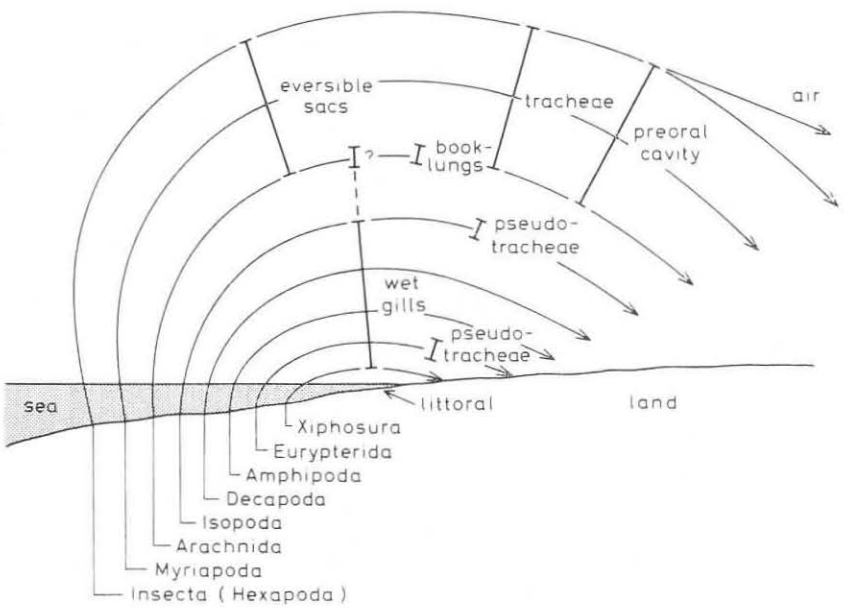
The vertebrates met with the same problems of adaptation as did the arthropods: mainly desiccation and change of respiration. It is tempting to draw a parallel between the development of the mouth cavity in vertebrates and the preoral cavity in arthropods. In fishes the mouth cavity is situated in front of the pharynx and is, thus, analogous with the preoral cavity in arthropods. The mouth cavity is filled with water which passes on to the gills, and therefore the water in the mouth is steadily changed. In this case enzymes may have little chance to play an important part in digestion of the prey in the mouth cavity. The digestion in actinopterygian fishes seems to resemble that of the crustaceans and merostomes. However, the air-breathing crossopterygians and dipnoans with their choanes have no permanent water-current running through the mouth to the respiratory organs. The enzymes have a satisfactory non-moving liquid environment through which they can pass from the pharynx to the chopped prey (at least the dipnoans with their blunt teeth are able to crush the prey into smaller pieces). It is beyond the scope of the present paper to evaluate in more

detail the analogy suggested above. *It seems possible, however, that at least one of the final adaptations towards the conquest of the land by arthropods and vertebrates, was the formation of a closeable cavity (preoral or mouth cavity) in front of the pharynx.*

General conclusions.

During the Silurian and early Devonian we may see among the arthropods many attempts to achieve by trial and error satisfactory adaptations to terrestrial life. The xiphosurans probably were able to frequent the intertidal or nearshore flats, whereas the eurypterids might have been more successful in being able to visit also the supralitoral zone (text-fig. 107). Both groups kept their gills wet but as we have seen it is possible that the eurypterids also possessed trachea-like respiratory organs.

Among the crustaceans the amphipods and decapods also breathed by protected wet gills, but still they were able to develop true terrestrial forms. The isopods have tried several different ways of adaptation: In addition to protected wet gills we find other ways of air-breathing, culminating in the development of complicated pseudotracheae. Certain isopods became true terrestrial forms. In the arachnids we find both book-lungs and tracheae, both successful adaptations to true terrestrial life. At the same time a preoral cavity is developed.



Text-fig. 107. Diagram indicating the invasion of land by different arthropod groups. Certain groups such as Xiphosura paid occasional visits to the intertidal zone whereas others became more permanent inhabitants of the land and even the air.

The myriapods possess a primitive, possibly respiratory organ in the ventral or coxal sacs. However, the more important terrestrial respiration is taken over by tracheae which evidently developed independently in several major groups. A preoral cavity is formed in the myriapods and is characteristic also of the insects, the latter developing elaborate tracheal systems. The diagram (text-fig. 107) indicates different steps towards the invasion of the land by the arthropods.

Literature.

ALEXANDER, A., & EWER, D. W. (1955): A note on the function of the eversible sacs of the onychophoran, *Opisthopatus cinctipes* PURCELL. — Ann. Natal. Mus., 13: 217-222; London, Dorking.

ANDERSON, D. T. (1973): Embryology and phylogeny in annelids and arthropods. — 495 pp., 164 text-figs.; London (Pergamon Press).

ANDREWS, H. E., & BROWER, J. C., & GOULD, S. J., & REYMENT, R. A. (1974): Growth and variation in *Eurypterus remipes* DEKAY. — Bull. geol. Inst. Univ. Uppsala, N. S., 4: 81-114, 16 text-figs.; Uppsala.

BARNES, D. B. (1963): Invertebrate zoology. — 632 pp., 20 text-fig. groups; Philadelphia, London (W. B. Saunders).

BERGSTROM, J. (1973): Organization, life and systematics of trilobites. — Fossils and strata, 2: 1-69, 16 text-figs., 5 pls.; Oslo.

BLISS, D. E. (1968): Transition from water to land in decapod crustaceans. — Amer. Zoologist, 8: 355-392, 21 text-figs.; Utica N. Y.

BLISS, D. E., & MANTEL, L. H. (1968): Adaptations of crustaceans to land: A summary and analysis of new findings. — Amer. Zoologist, 8: 673-685; Utica N. Y.

BORNER (1901): Zur äusseren Morphologie von *Koenia mirabilis grassi*. — Zool. Anz., 24: 537-556, 11 text-figs.; Marburg.

BURKE, J. J. (1973): Notes on the morphology of *Acantherpestes* (Myriapoda, Archipolypoda) with the description of a new species from the Pennsylvanian of West Virginia. — Kirtlandia, Cleveland Mus. natur. Hist., 17: 1-27, 7 text-figs.; Cleveland Ohio.

CLARIDGE, M. F., & LYON, S. G. (1961): Lung-books in the Devonian Palæocharinidae (Arachnida). — Nature, 191 (4794): 1190-1191; London.

CLARKE, J. M., & RUEDEMANN, R. (1912): The Eurypterida of New York. — N. Y. State Mus., Mem., 14: 1-439, 121 text-figs., 88 pls.; Albany N. Y.

DALINGWATER, J. E. (1973): The cuticula of a eurypterid. — Lethaia, 6: 179-186, 4 text-figs.; Oslo.

DENNEL, R. (1934): The feeding mechanism of the cumacean crustacean *Diastylis bradyi*. — Trans. roy. Soc. Edinburgh, 58: 125-142, 9 text-figs.; Edinburgh.

DORJES, J. (1970): Das Watt als Lebensraum. — In: REINECK, H.-E. [Ed.], Das Watt, Ablagerungs- und Lebensraum: 71-105, text-figs. 53-61; Frankfurt am Main (Kramer).

DOHLE, W. (1974): The segmentation of the germ band of Diplopoda compared with other classes of arthropods. — Symp. zool. Soc. London, 32: 143-161, 9 text-figs.; London.

EDNEY, E. B. (1960): Terrestrial adaptations. — In: WATERMAN, T. H. [Ed.], The physiology of Crustacea, 1: 376-393; New York, London (Academic Press).

EMERY, K. O. (1969): A coastal pond studied by oceanographic methods. — Amer. Elsevier Publ., 80 pp., 41 text-figs.; New York.

EMERY, K. O., & STEVENSON, R. E. (1957): Estuaries and lagoons. I. Physical and chemical characteristics. In: HEDGPETH, J. W. [Ed.], Treatise on marine ecology and paleoecology, 1. — Geol. Soc. Amer., Mem., 67: 673-749, 30 text-figs.; Boulder Colo.

FAHLBUSCH, K. (1960): Eine Pteraspiden-Fauna aus dem Unterdevon von Alken an der Mosel. — Senckenbergiana lethaea, 47: 165-191, 24 text-figs., pls. 17-20; Frankfurt am Main.

FRITSCH, A. (1899): Fauna der Gaskohle und der Kalksteine der Permformation Böhmens. — Prag.

HANKEN, N. M., & STØRMER, L. (1975): Tracks of a larger eurypterid. — Fossils and strata, 4: 255-270, 12 text-figs., 3 pls.; Oslo.

HEFTER, J. (1973): Fischfossilien des rheinischen Unterdevons. — Der Aufschluß, Jg. 24 (10): 378-380; Heidelberg.

HENRIKSEN, K. L. (1932): The manner of moulting in Arthropoda. — Notula entomol., 11 [1931]: 103-127, 14 text-figs.; Copenhagen.

HEIDE, S. VAN DER (1951): Les arthropodes du Terrain Houiller du Limbourg Méridional. — Meded. geol. Stichting, Serie C-IV-3-No 5 [New Sec. Ser. C]: 1-84, 10 pls.; s'Gravenhage.

HIRST, S. (1923): On some arachnid remains from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire). — Ann. Mag. natur. Hist., (9) 12: 455-474, 13 text-figs.; London.

HOFFMANN, R. L. (1969): Myriapods, exclusive of Insecta. — In: MOORE, R. C. [Ed.], Treatise invertebr. Paleont., P. *R*, Arthropoda 4: 572-606, text-figs. 314-385; Lawrence Kans.

HOLM, G. (1898): Ueber die Organisation des *Eurypterus Fischeri* EICHW. — Mém. Acad. imp. Sci. St. Petersbourg, (8) 8 (2): 1-57, pls. 1-10; St. Petersbourg.

HUGHES, N. F., & SMART, J. (1967): Plant-insect relationships in Palaeozoic and later time. — In: HARLAND, W. B., & al. [Ed.], The fossil record: 107-117; London.

HURLEY, D. E. (1968): Transition from water to land in amphipod crustaceans. — Amer. Zoologist, 8: 327-353, 11 text-figs.; Utica N. Y.

JAEKEL, O. (1914): Ein großer *Pterygotus* aus dem rheinischen Unterdevon. — Paläont. Z., 1: 379-382, 4 text-figs.; Berlin.

JORDAN, H., & MEYER, H. (1854): Ueber die Crustaceen der Steinkohlenformation von Saarbrücken. — Palaeontographica, 4: 1-15, 2 pls.; Cassel.

KÄSTNER, A. (1925): Vergleichend-morphologische Untersuchungen der Gnathocoxen der Araneen. — Z. Morphol. Ökol. Tiere, 4: 711-738, 35 text-figs.; Berlin.

— — — (1940a): Arachnida. — In: KÜKENTHAL, W., & KRUMBACH, T. [Ed.], Handb. Zool., 3 (2): 97-116, text-figs. 75-87; Berlin.

— — — (1940b): Scorpiones. — In: KÜKENTHAL, W., & KRUMBACH, T. [Ed.], Handb. Zool., 3 (2): 117-240, text-figs. 89-222; Berlin.

— — — (1949): Zur Entwicklungsgeschichte von *Thelyphonus caudatus* L. (Pedipalpi). 2. Teil. Die Entwicklung der Mundwerkzeuge, Beinhüften und Sterna. — Zool. Jb., Abt. Anat. Ontogen., 70: 169-197, 37 text-figs.; Jena.

— — — (1959): Lehrbuch der speziellen Zoologie. — Tl. 1, Wirbellose, 4. Lfg.: 653-979, 232 text-figs.; Jena.

— — — (1968): Invertebrate Zoology. — 2 [translated and adapted from the German by LEVI, H. W., & LEVI, L. R.]: 472 pp., 223 text-figs.; New York (Wiley).

KAUTSCH, G. (1910): Über die Entwicklung von *Aegelena labyrinthica*. — Zool. Jb. Anat., **30**: 536-602, pls. 30-34, text-figs. 1-29; Jena.

KEVAN, P. G., & CHALONER, W. G., & SAVILLE, D. B. O. (1975): Interrelationships of early terrestrial arthropods and plants. — Palaeontology, **18** (2): 391-417, pls. 54-56; London.

KIDSTONE, R., & LANG, W. H. (1921): On Old Standstone plants showing structures, from the Rhynie Chert Bed, Aberdeenshire. Part 5. The Thallophyte occurring in the peat-bed; the succession of the plants throughout a vertical section of the bed, and the conditions of accumulation and preservation of the deposit. — Trans. roy. Soc. Edinburgh, **52** (4): 855-902, 1 text-fig., 10 pls.; Edinburgh.

KJELLESVIG-WAERING, E. N. (1951): Downtonian (Silurian) Eurypterida from Perton, near Stoke Edith, Herefordshire. — Geol. Mag., **87**: 1-24, 3 pls.; London.

— — — (1958): The genera, species and subspecies of the family Eurypteridae, BURMEISTER, 1845. — J. Paleont., **32** (6): 1107-1148, 27 text-figs., pls. 94-96; Tulsa Okla.

— — — (1961a): The Silurian Eurypterida of the Welsh Borderland. — J. Paleont., **35** (4): 789-835, 4 text-figs., pls. 94-96; Tulsa Okla.

— — — (1961b): Eurypterids of the Devonian Holland Quarry Shale of Ohio. — Fieldiana, Geol., **1105**: 79-98, text-figs. 35-53; Chicago Ill.

— — — (1966): A revision of the families and genera of the Stylonuracea (Eurypterida). — Fieldiana, geol. Publ. Chicago, natur. Hist. Mus., **14** (5): 169-197, 4 text-figs.; Chicago Ill.

— — — (1972): *Brontoscorpio anglicus*: A gigantic Lower Paleozoic scorpion from Central England. — J. Paleont., **46**: 39-42, 2 text-figs.; Tulsa Okla.

KRAUSEL, R., & WEILAND, H. (1930): Die Flora des deutschen Unterdevons. — Abh. preuß. geol. L.-Anst., N. F., **131**: 1-92, 92 text-figs., 14 pls.; Berlin.

KRAUS, O. (1974): On the morphology of Palaeozoic diplopods. — Symp. Zool. London, No. 32: 13-22, text-figs. 1-4; London.

LAWRENCE, R. F. (1953): The biology of the cryptic fauna of forests. — 408 pp., 160 text-figs.; Cape Town, Amsterdam (Balkema).

MANTON, S. M. (1954): The evolution of the arthropodan locomotory mechanisms. Part 4. The structure, habits and evolution of the Diplopoda. — J. Linnean Soc., Zool., **42**: 299-368, 8 text-figs., 4 pls.; London.

— — — (1958): The evolution of the arthropodan locomotory mechanisms. Part 6. Habits and evolution of the Lysiopetaloidea (Diplopoda), some principles of the leg design in Diplopoda and Chilopoda, and limb structures in Diplopoda. — J. Linnean Soc., Zool., **43**: 487-536, 21 text-figs., 1 pl.; London.

— — — (1965): The evolution of arthropodan locomotory mechanisms. Part 8. Functional requirements and body designs in chilopods together with comparative account of their skeleto-muscular systems, and appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan haemocoel. — J. Linnean Soc., Zool., **46**: 251-483, 99 text-figs., 7 pls.; London.

— — — (1972): The evolution of arthropodan locomotory mechanisms. Part 10. Locomotory habits, morphology and evolution of the hexapod classes. — J. Linnean Soc., Zool., **51**: 203-400, 40 text-figs., 6 pls.; London.

— — — (1973): The evolution of arthropodan locomotory mechanisms. Part 11. Habits, morphology and evolution of the Uniramia (Onychophora, Myriapoda, Hexapoda) and comparisons with Arachnida, together with a functional review of uniramian musculature. — J. Linnean Soc., Zool., **53**: 257-275, 19 text-figs., 3 pls.; London.

Millot, J. (1949): Classe des Arachnides. — In: Grassé, P. P. [Ed.], Traité Zool., **6**: 261-793, text-figs. 47-579; Paris.

Moore, P. F. (1941): On gill-like structures in the Eurypterida. — Geol. Mag., **78**: 62-70, 2 text-figs.; London.

Niehoff, W. (1958): Die primär gerichteten Sedimentstrukturen, insbesondere die Schrägschichtung im Koblenzquarzit am Mittelrhein. — Geol. Rdsch., **47**: 252-321, 39 text-figs., pl. 9; Stuttgart.

Pavlovski, R. (1926): Studies on the organization and development of scorpions. 5. The lungs. — Quart. J. microsc. Sci., **70**: 135-146, pls. 12-13; London.

Peach, B. N. (1883): On some fossil myriapods from the Lower Old Red Sandstone of Forfarshire. — Proc. roy. phys. Soc. Edinburgh, **7**: 177-180, 1 pl.; Edinburgh.

Petrunkevitch, A. (1949): A study of Palaeozoic Arachnida. — Connecticut Acad. Arts, Sci. Trans., **18**: 137 pp., 83 pls.; New Haven Conn.

— — — (1955): Arachnida. — In: Moore, R. C. [Ed.], Treatise invertebr. Paleont., P. *R*, Arthropoda 4: 42-162, text-figs. 31-116; Lawrence Kans.

Pocock, R. (1911): A monograph of terrestrial Carboniferous Arachnida of Great Britain. — Palaeontograph. Soc. [1910]: 84 pp., 42 text-figs., 3 pls.; London.

Raymond, P. E. (1920): The appendages, anatomy and relationships of Trilobita. — Mem. Connecticut Acad. Arts Sci., **4**: 1-169, 46 text-figs., 11 pls.; New Haven Conn.

Richardson, E. S. (1956): Pennsylvanian invertebrates of the Mazon Creek area, Illinois. Trilobitomorpha, Arthropleurida. — Fieldiana, Geol., **12**: 69-76, text-figs. 38-41; Chicago Ill.

Richter, Rud. (1931): Tierwelt und Umwelt im Hunsrückschiefer; zur Entstehung eines schwarzen Schlammsteins. — Senckenbergiana, **13** (5/6): 299-342, 16 text-figs.; Frankfurt am Main.

Rolfe, W. D. J. (1969): Arthropleurida. — In: Moore, R. C. [Ed.], Treatise invertebr. Paleont., P. *R*, Arthropoda 4: 607-620, text-figs. 386-393; Lawrence Kans.

Rolfe, W. D. J., & Ingham, J. K. (1967): Limb structure, affinities and diet of the Carboniferous "Centipede" *Arthropleura*. — Scott. J. Geol., **3**: 118-124, 2 text-figs., 1pl.; Edinburgh.

Romer, A. S. (1966): Vertebrate Paleontology. — I-VIII + 468 pp., 443 text-figs.; Chicago (Univ. Chicago Press).

Ruedemann, R. (1921): Preservation of alimentary canal in an eurypterid. — Paleont. Contr., New York State Mus. Bull. 227/228: 92-95, text-figs. 33-35; Albany N. Y.

Scourfield, D. J. (1926): On a new type of Crustacean from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire), *Lepidocaris rhyniensis* gen. et sp. nov. — Philos. Trans. roy. Soc. London., (B) **214**: 153-187, 51 text-figs., 3 pls.; London.

— — — (1940): The oldest known fossil insect (*Rhyniella praecursor* Hirst and Manlik). Further details from additional specimens. — Proc. Linnean Soc. London, 152th Sess.: 113-131, 10 text-figs.; London.

Schaarschmidt, F. (1970): Beziehungen zwischen der Entstehung der Kormophyten und dem Übergang der Pflanzen vom Wasser- zum Landleben. — Wiss. Z. Friedrich-Schiller-Univ. Jena, math.-naturwiss. R., 19. Jg. [1970] (3): 419-426, 4 text-figs.; Jena.

— — — (1974): *Mosellophyton hefteri* n. g. n. sp. (? Psilophyta), ein sukkulenter Halophyt aus dem Unterdevon von Alken an der Mosel. — Paläont. Z., **48** (3/4): 188-204, 4 text-figs., pls. 28-29; Stuttgart.

SHAROV, A. B. (1966): Basic arthropodan stock with special reference to insects. — 271 pp., 89 text-figs.; London (Pergamon Press).

SNODGRASS, R. E. (1950): Comparative studies on the jaws of mandibulate arthropods. — Smithsonian misc. Coll., **116**: 1-85, 25 text-figs.; Washington D. C.

— — — (1952): A text-book of arthropod anatomy. — 363 pp., 88 text-figs.; Ithaca N. Y. (Comstock Publ. Assoc.).

SOLLE, G. (1970): Die Hunsrück-Insel im oberen Unterdevon. — Notizbl. hess. L.-Amt. Bodenforsch., **98**: 50-80, 1 text-fig., 6 pls.; Wiesbaden.

STØRMER, L. (1934): Merostomata from the Downtonian Sandstone of Ringerike, Norway. — Skr. norske Vid.-Akad., Oslo, I, mat.-naturvid. Kl., 1933, Nr. 10: 1-125, 39 text-figs., 12 pls.; Oslo.

— — — (1935): *Dictyocaris* SALTER, a large crustacean from the Upper Silurian and Downtonian. — Norsk geol. T., **15**: 265-298, 4 text-figs., 4 pls.; Oslo.

— — — (1936): Eurypteriden aus dem Rheinischen Unterdevon. — Abh. preuß. geol. L.-Anst., N. F., **175**: 1-74, 10 text-figs., 12 pls.; Berlin.

— — — (1939): Studies on trilobite morphology. Part 1. The thoracic appendages and their phylogenetic significance. — Norsk geol. T., **19**: 143-273, 35 text-figs., 12 pls.; Oslo.

— — — (1959): Arthropoda - general features. — Treatise invertebr. Paleont., P. O, Arthropoda 1: 3-15, 10 text-figs.; Lawrence / Kans.

— — — (1963): *Gigantoscorpio willsi*, a new scorpion from the Lower Carboniferous of Scotland and its associated preying microorganisms. — Skr. norske Vid.-Akad., Oslo, I, mat.-naturvid. Kl., N. S., **8**: 1-171, 45 text-figs., 22 pls.; Oslo.

— — — (1970): Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 1: Arachnida. — Senckenbergiana lethaea, **51** (4): 335-369, 8 text-figs., 5 pls.; Frankfurt am Main.

— — — (1972): Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 2: Xiphosura. — Senckenbergiana lethaea, **53** (1/2): 1-29, 23 text-figs., 6 pls.;Frankfurt am Main.

— — — (1973): Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 3: Eurypterida, Hughmilleriidae. — Senckenbergiana lethaea, **54** (2/4): 119-205, 97 text-figs., 6 tables, 13 pls.; Frankfurt am Main.

— — — (1974): Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 4: Eurypterida, Drepanopteridae, and other groups. — Senckenbergiana lethaea, **54** (5/6): 359-451, 45 text-figs., 3 tables, 16 pls.; Frankfurt am Main.

STØRMER, L., & WATERSTON, CH. (1968): *Cyrtoctenus* gen. nov., a large late Paleozoic arthropod with pectinate appendages. — Trans. roy. Soc. Edinburgh, **68** (4): 63-104, 14 text-figs., pls. 68-88; Edinburgh.

Symposium on terrestrial adaptations in Crustacea (1968). — Amer. Zool., **8** (3): 327-685; New York.

TIEGS, O. W. (1940): The embryology and affinities of the Symphyla, based on a study of *Hanseniella agilis*. — Quart. J. microsc. Sci., **82**: 1-225, 41 text-figs., 9 pls.; London.

UNWIN, E. E. (1932): On the structure of respiratory organs of terrestrial Isopoda. — Pap. Proc. roy. Soc. Tasmania, 1931: 37-97, 71 text-figs., 8 pls.; Hobart.

VOGEL, B. R., & DURDEN, C. J. (1966): The occurrence of stigmata in a Carboniferous scorpion. — J. Paleont., **40** (3): 655-658, 2 text-figs., pl. 81; Tulsa Okla.

WATERLOT, G. (1934): Études des gites minéraux de la France Bassin Houiller de la Sarre et de la Lorraine. II. Faune fossile. Étude de la faune continental du Terrain Houiller Sarro-Lorrain. — 317 pp., 61 text-figs., 24 pls.; Lille.

— — — (1949): Découverte de deux fragmentes de patte-machoire d'*Arthropleura* (archeocrustacé) du Terrain Houiller Sarro-Lorrain. — Ann. Soc. geol. Nord, 67: 183-195, 4 text-figs., pl. 6; Lille.

WATERSTON, CH. D. (1964): Observations on pterygotic eurypterids. — Trans. roy. Soc. Edinburgh, 66: 9-33, 5 text-figs., 4 pls.; Edinburgh.

— — — (1975): Gill structures in the Lower Devonian eurypterid *Tarsopterella scotica*. — Fossils and strata, 4: 241-254, 4 text-figs., 4 pls.; Oslo.

WATERSTON, CH., & WEIDMANN, C. (1967): Ein neuer Eurypteriden-Fund in der Eifel. — Mitt. Ruhrland-Mus. Stadt Essen, No. 194; Glückauf, Jg. 103 (1): 43, 44, 3 text-figs.; Essen.

WILLS, L. J. (1946): A monograph of British Triassic scorpions. Part 1. — Palaeontogr. Soc., 1946: 1-137, 53 text-figs., 10 pls.; London.

— — — (1965): A supplement to GERHARD HOLM's "Über die Organisation des *Eurypterus Fischeri* EICHW.", with special reference to the organs of sight, respiration and reproduction. — Ark. Zool. kgl. svensk. Ved.-Akad., (2) 18 (2): 93-145, 19 text-figs., 5 pls.; Stockholm.

WOODWARD, H. (1866-1878): Monograph of the British fossil Crustacea belonging to the order Merostomata. — Paleontogr. Soc. London: 1-263, 81 text-figs., 36 pls.; London.

WUNDERLICH, F. (1966): Genese und Umwelt der Nellenköpfchenschichten (oberes Unterems, Rhein. Devon) am locus typicus im Vergleich mit der Küstenfacies der deutschen Bucht. — Diss. Univ. Frankfurt; Frankfurt am Main. — (Type-written.)

— — — (1970): Genesis and environment of the "Nellenköpfchenschichten" (Lower Emsian, Rheinian Devon) at locus typicus in comparison with modern coastal environment of the German Bay. — J. sedim. Petrol., 40 (1): 102-130, 42 text-figs.; Tulsa Okla. — (Detailed summary of the 1966 paper.)

ZANGERL, R. & RICHARDSON, E. (1963): The paleoecological history of two Pennsylvanian black shales. — Fieldiana: Geol. Mem., 4: 1-352, 51 text-figs., 54 pls.; Chicago Ill.

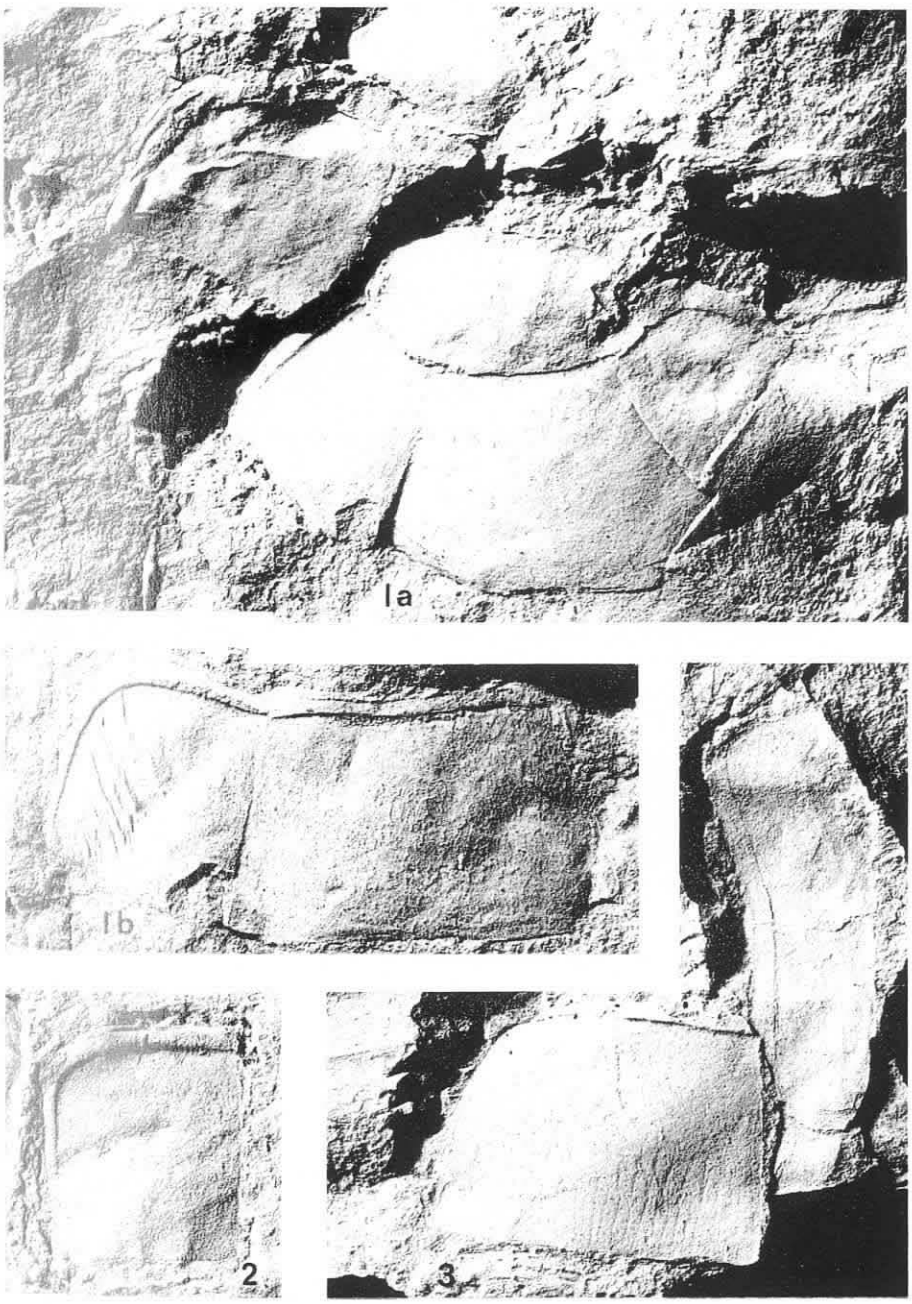
Plate 1.

Eoarthropleura devonica n. g., n. sp. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

Fig. 1. Holotype, head and tergites; SMF VIII 282a, b; × 3, whitened (text-figs. 6-7). — a) head with first tergite of the trunk. — b) probably second tergite of holotype.

Fig. 2. Paratype, paratergal fold; SMF VIII 302; × 3, whitened.

Fig. 3. Paratype; to the right tergal and paratergal fold in which the posterior portion (corresponding to the area of the doublure) is missing; to the left paratergal fold with impressions of the corrugated dorsal surface of the doublure; SMF VIII 263; × 3, whitened.



L. STØRMER: Arthropods (myriapods and additional forms) from the Lower Devonian of Alken an der Mosel.

Plate 2.

Eoarthropleura devonica n. g., n. sp. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

Fig. 1. Paratype, tergite of a younger specimen; SMF 30038; × 5·5, whitened (text-fig. 9).

Fig. 2. Paratype, shriveled paratergal fold; SMF 30044; × 6, whitened.

Fig. 3. Paratype, tergite with slightly dislocated left paratergal fold; impressions of corrugated surface of doublure demonstrated; SMF 30045; × 4, whitened.

Fig. 4. Paratype, paratergal fold; SMF 30037; × 4, whitened.

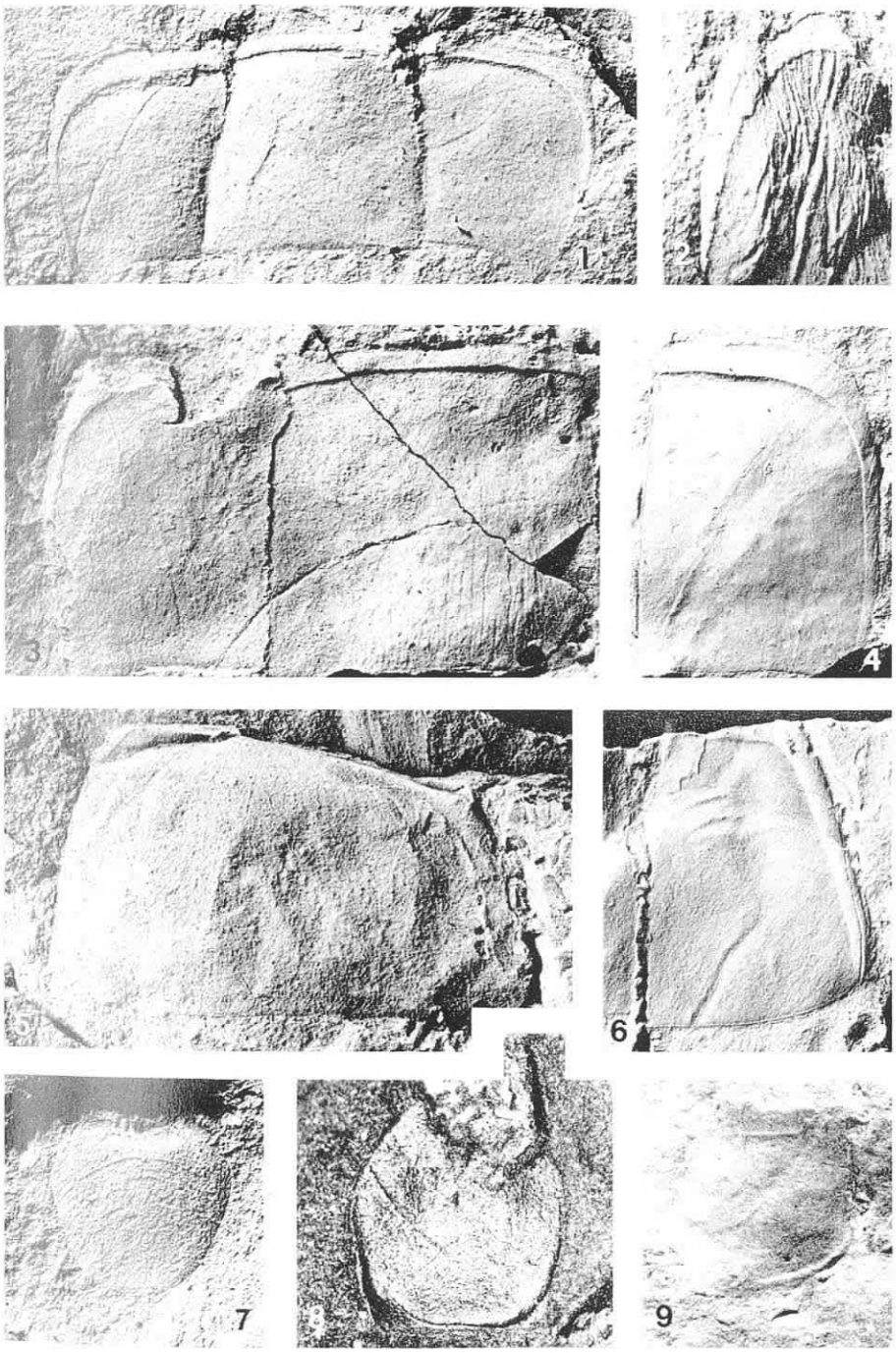
Fig. 5. Paratype, possibly tergite with paratergal fold; SMF VIII 285; × 4·1, whitened.

Fig. 6. Paratype, paratergal fold with suture (?) on marginal rim; SMF 30039; × 4·1, whitened.

Fig. 7. Paratype, cordate plate interpreted as a labrum; SMF VIII 300b; × 5, whitened (text-fig. 16).

Fig. 8. Paratype, sternite; SMF VIII 287a; × 5·2 (text-fig. 19).

Fig. 9. Paratype, sternite; SMF VIII 286; × 4·9, whitened.



L. STØRMER: Arthropods (myriapods and additional forms) from the Lower Devonian of Alken an der Mosel.

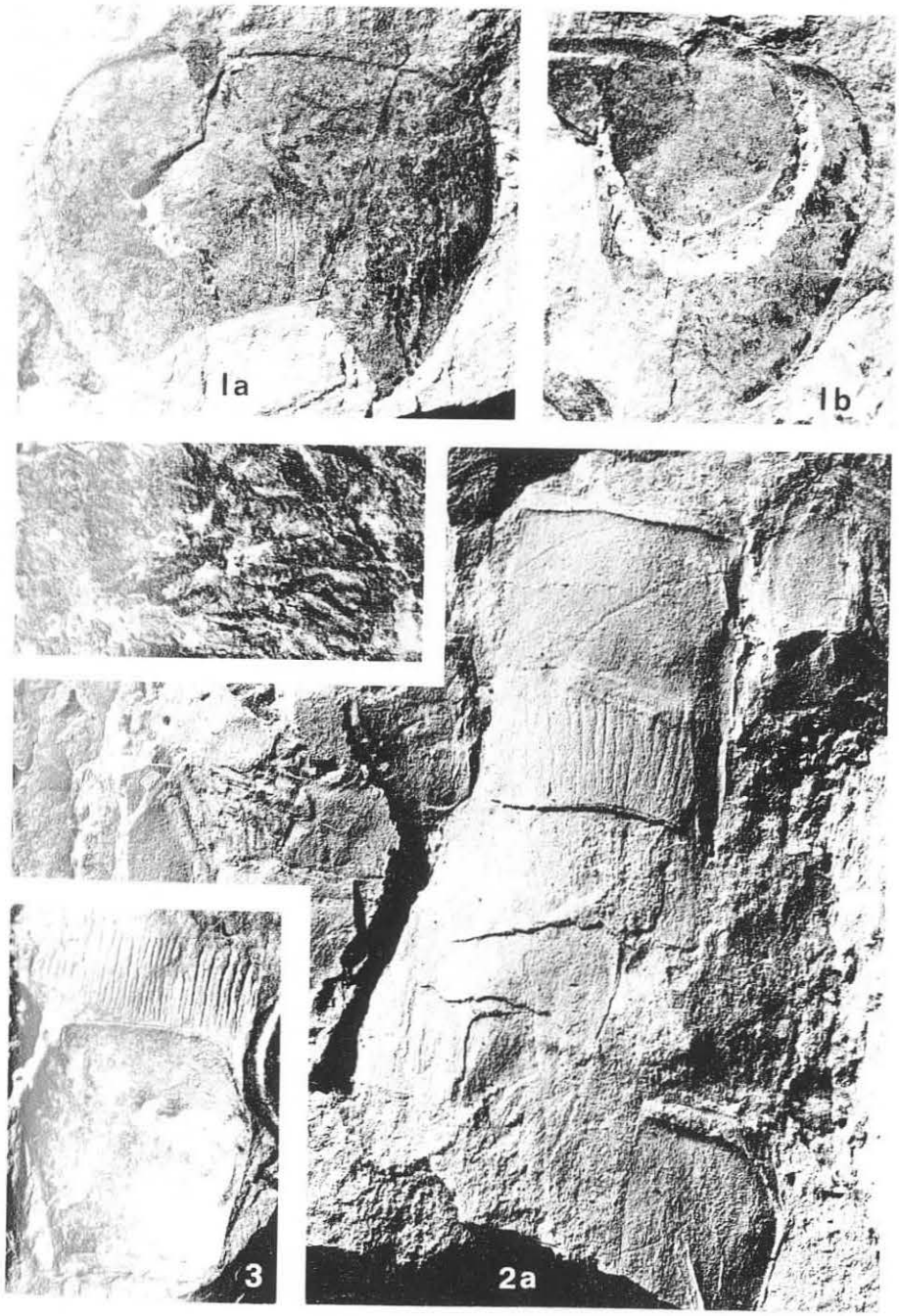
Plate 3.

Eoarthropleura devonica n. g., n. sp. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

Fig. 1. Paratype, posterior, pobably penultimate tergite of the trunk; SMF VIII 246; × 3·6 (text-figs. 12, 20). — a) tergite. — b) tergite, with sternite preserved.

Fig. 2. Paratype, remains of five succeding tergites with traces of appendages to the left; SMF 30043. — a) specimen × 3·5, whitened (text-fig. 11). — b) specimen × 8.

Fig. 3. Paratype, sternite with doublure of tergite in front; SMF VIII 248; × 4·5.



L. STORMER: Arthropods (myriapods and additional forms) from the Lower Devonian of Alken an der Mosel.

Plate 4.

Eoarthropleura devonica n. g., n. sp. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

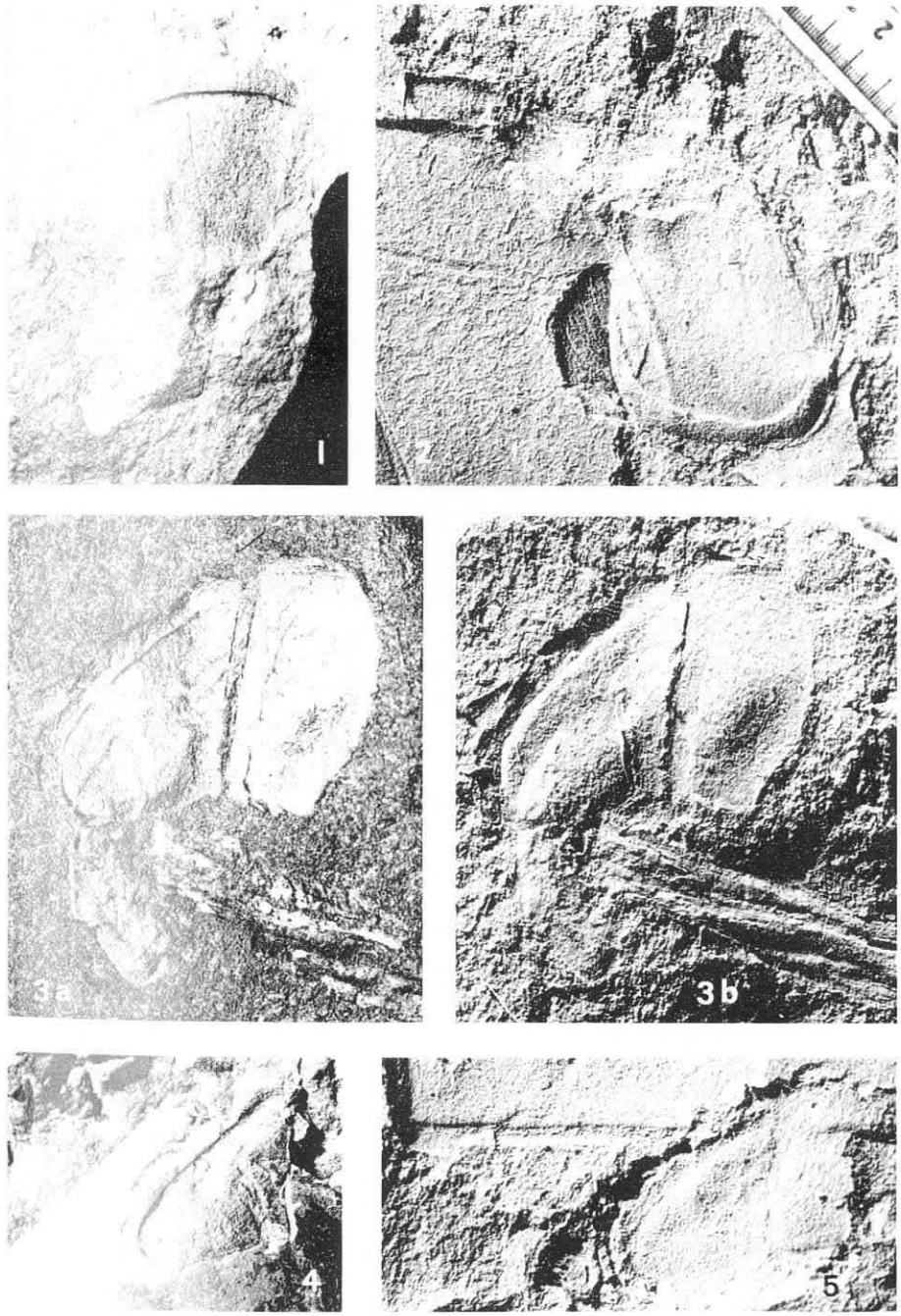
Fig. 1. Paratype, probably last narrow tergite with long paratergal fold; SMF VIII 290; × 5·1 (text-fig. 13).

Fig. 2. Paratype, fragment of tergite with sternite; the sternite has later been removed to expose a presumed labrum of which only a narrow striated portion is shown in the present fig. (this plate is shown in pl. 8 fig. 2); SMF VIII 300a; × 5·4, whitened (text-figs. 15, 18).

Fig. 3. Paratype, B- and K-plate with fragments of an appendage; SMF VIII 303b; × 5 (text-fig. 21). — a) Specimen not whitened. — b) Specimen whitened.

Fig. 4. Paratype, B-plate; SMF 30045; × 5·1.

Fig. 5. Paratype, A- and B-plate; SMF VIII 300b; × 5, whitened.



L. STØRMER: Arthropods (myriapods and additional forms) from the Lower Devonian of Alken an der Mosel.

Plate 5.

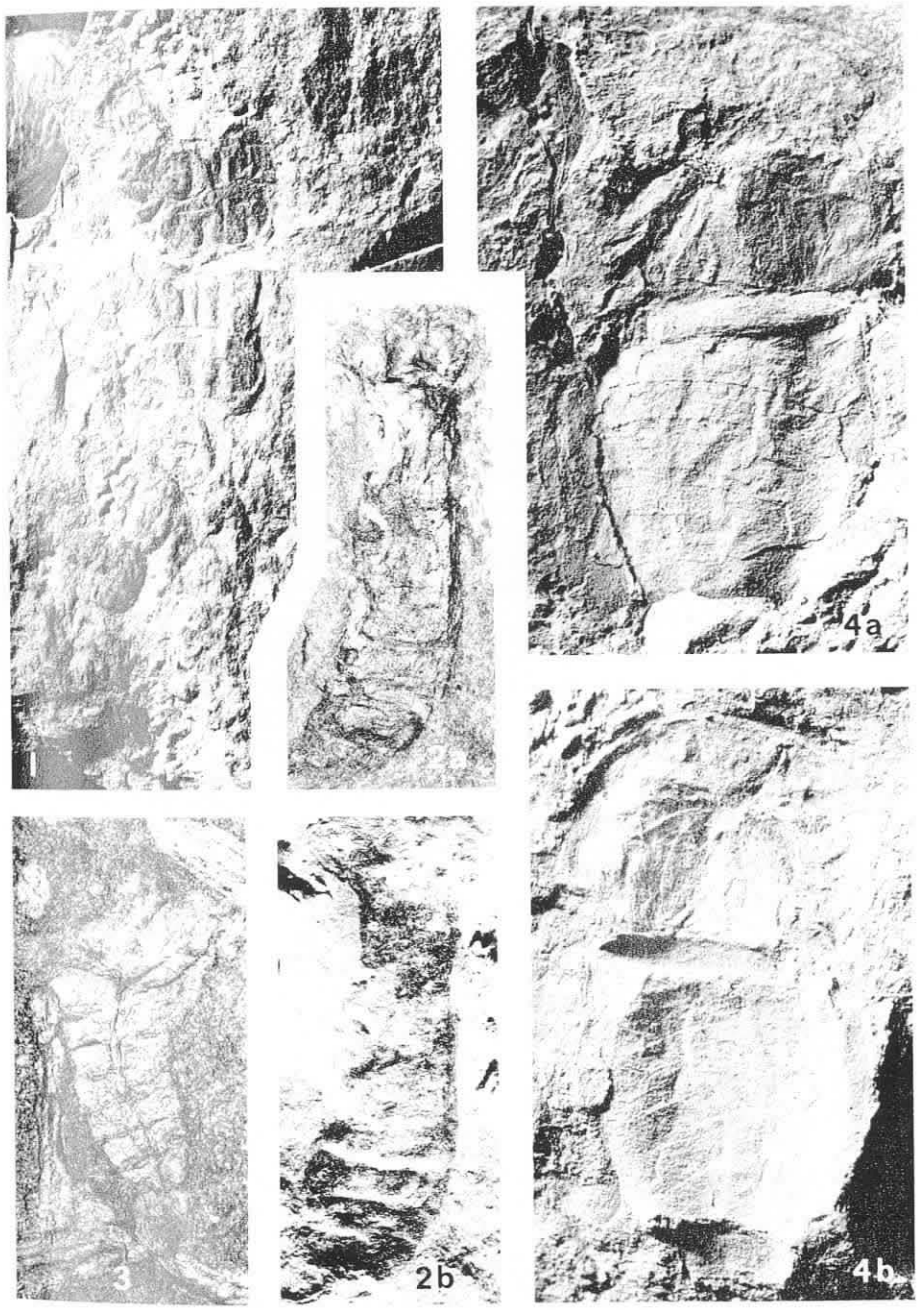
All specimens from: Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

Fig. 1. Scorpionidorum g. et sp. indet. — SMF 30047; × 3, whitened (text-fig. 47).

Fig. 2. *Archaeometa ? devonica* n. g., n. sp. — Holotype, opisthosoma with traces of prosoma; SMF 30048; × 4 (text-fig. 48). — a) Specimen photographed in alcohol. — b) Specimen not whitened.

Fig. 3. Arthropodorum g. et sp. indet. — SMF 30048; × 4 (text-fig. 55).

Fig. 4. ? *Alkenopterus brevitelson* Stormer 1974. — Prosoma and mesosoma; × 5, whitened. — a) Specimen SMF VIII 284a. — b) Counterpart SMF VIII 284b.



L. STØRMER: Arthropods (myriapods and additional forms) from the Lower Devonian of Alken an der Mosel.

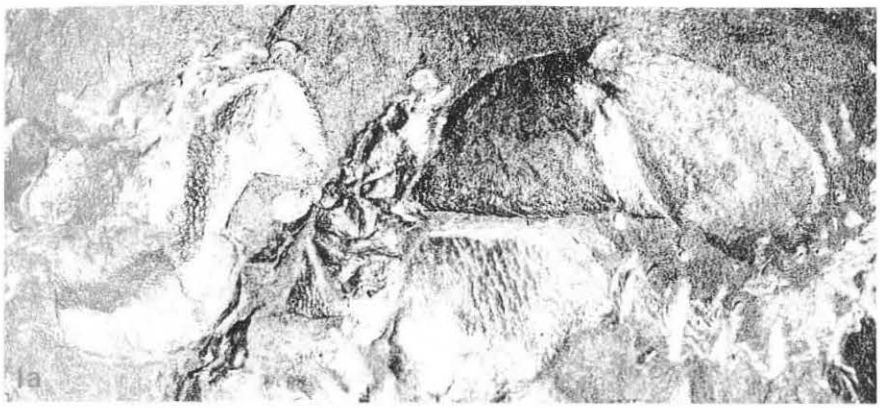
Plate 6.

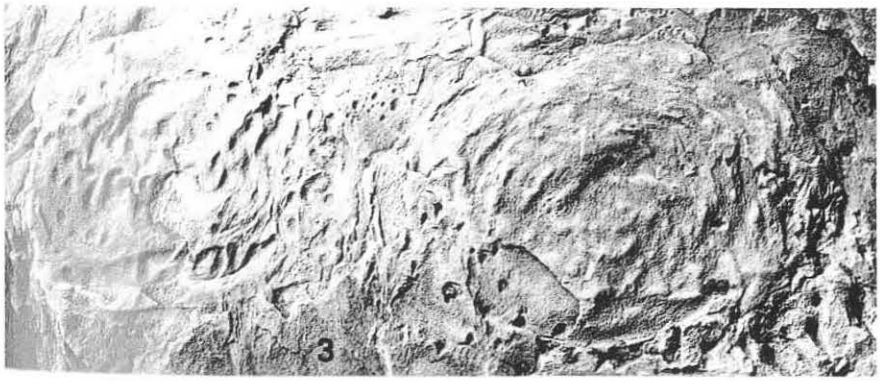
All specimens from: Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

Fig. 1. *Parahughmilleria hefteri* STORMER 1973, and *Parahughmilleria major* STORMER 1973. — Swimming legs; SMF 30049. — a) Coxa of swimming leg (VI) of *P. hefteri* to the left (text-fig. 50) and swimming leg of *P. major* to the right; × 4, photographed in alcohol. — b) Detail of coxa of *P. hefteri*; × 7·6.

Fig. 2. *Parahughmilleria hefteri* ? STORMER 1973. — Larval form with parts of prosomal appendages preserved; SMF 30051; × 5·2, photographed in alcohol.

Fig. 3. Merostomatidorum g. et sp. indet. — SMF 30050; × 3·5, whitened.





L. STØRMER: Arthropods (myriapods and additional forms) from the Lower Devonian of Alken an der Mosel.

Plate 7.

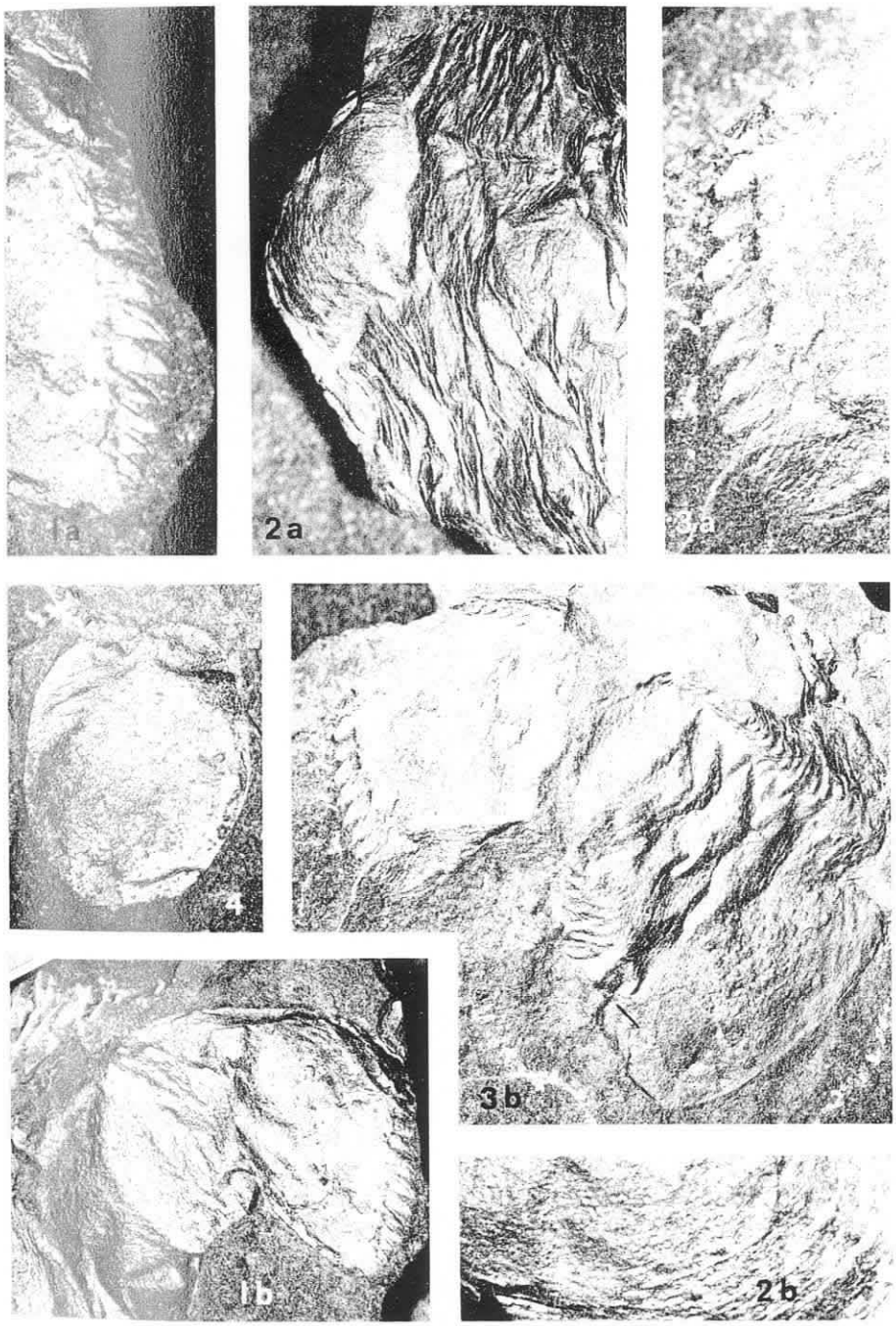
Jaekelopterus rhenaniae (JAEKEL 1914). — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

Fig. 1. Distal portion of coxa of swimming leg (VI); SMF 30053. — a) Specimen × 6. — b) Specimen × 3·5.

Fig. 2. Strongly shrivelled portion of prosoma; SMF 30053a; × 3·5. — a) Total view; × 3·5. — b) Detail of lateral eye showing facets; × 1·4.

Fig. 3. Distal portion of coxa of swimming leg (fig. 3b). — a) Dorsal view; SMF 30054b; × 6 (text-fig. 51b). — b) Ventral view; SMF 30054a; × 3·5.

Fig. 4. Metastoma; SMF 30054; × 3 (text-fig. 51a).



L. STORMER: Arthropods (myriapods and additional forms) from the Lower Devonian of Alken an der Mosel.

Plate 8.

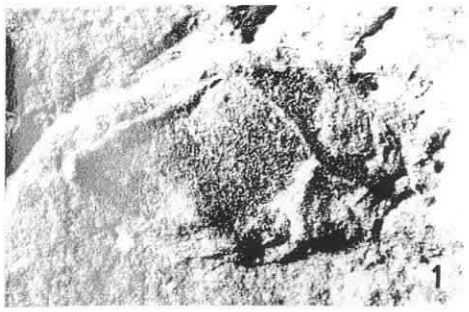
Figs. 1-2. *Eoarthropleura devonica* n. g., n. sp. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

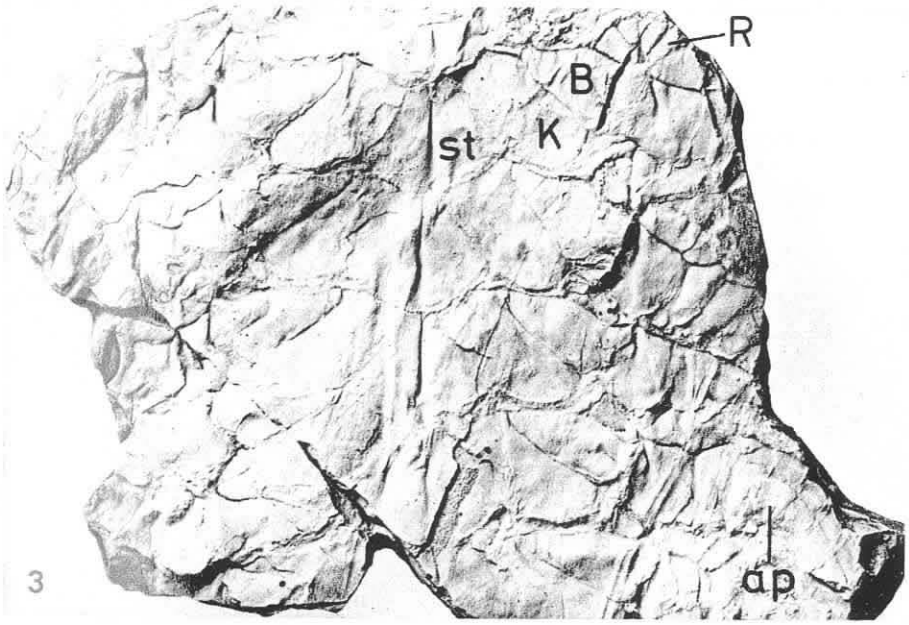
1. Paratype, small plate interpreted as mandible; SMF VIII 300a; × 11·4 (text-figs. 23a-b).
2. Paratype, cordate plate interpreted as labrum; SMF 300a; × 7·7 (text-fig. 17).

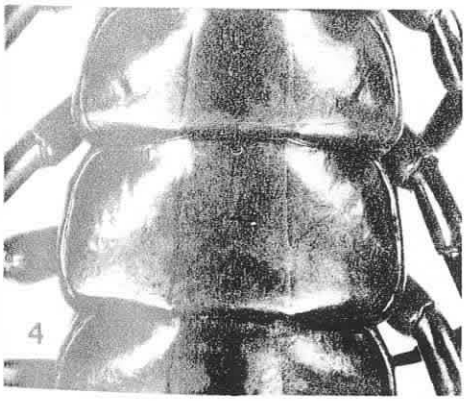
Fig. 3. *Arthropleura armata* JORDAN 1954. — Cast of a young specimen, showing ventral plates and appendages; Mus. Bergschule Saarbrücken; × 1, whitened (explanations of abbreviations see text-fig. 43). — Carboniferous, Westphalian; Brefeld Saar.

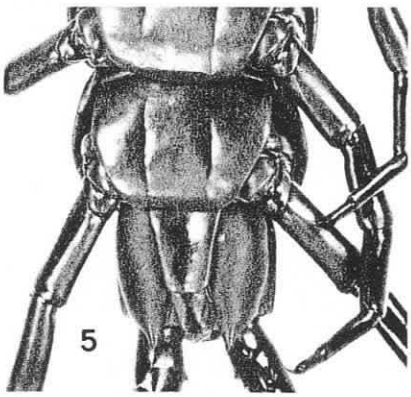
Figs. 4-5. Large centiped, *Scolopendra gigantea* LINNAEUS 1758. — Recent; Kronstadt Island, NW. Trinidad.

4. Tergites with dorsal axial furrows; × 2·1.
5. Ventral view of posterior segments with long paratergal folds; × 1·7.









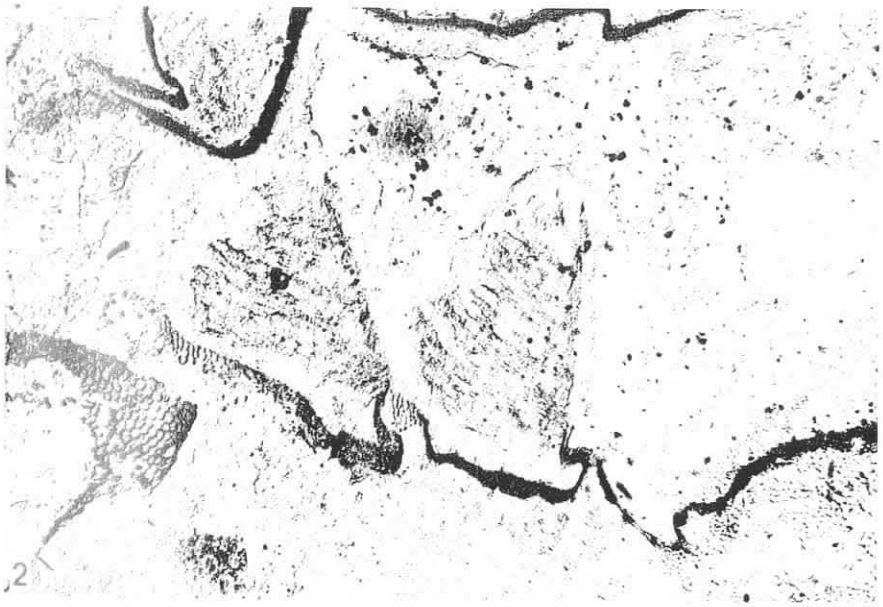
L. Størmer: Arthropods (myriapods and additional forms) from the Lower Devonian of Alken an der Mosel.

Plate 9.

Slides from the presumed Lower Devonian (Emsian ?) Rhynie Chert Bed; Aberdeenshire Scotland.

Figs. 1-2. Palaeocharinidae, g. et sp. indet. — (Photographs published in "Nature" by Claridge & Lyon 1961.)

1. Cross section showing position of book-lung, and sections of prosomal legs; about × 60 (?).
2. Longitudinal section of the anterior prosomal segments with book-lungs; × 200.

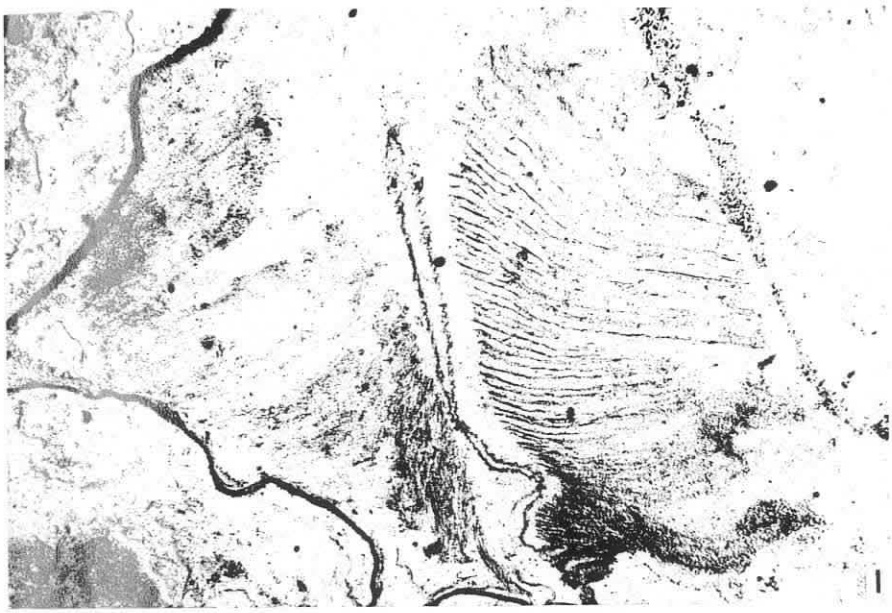


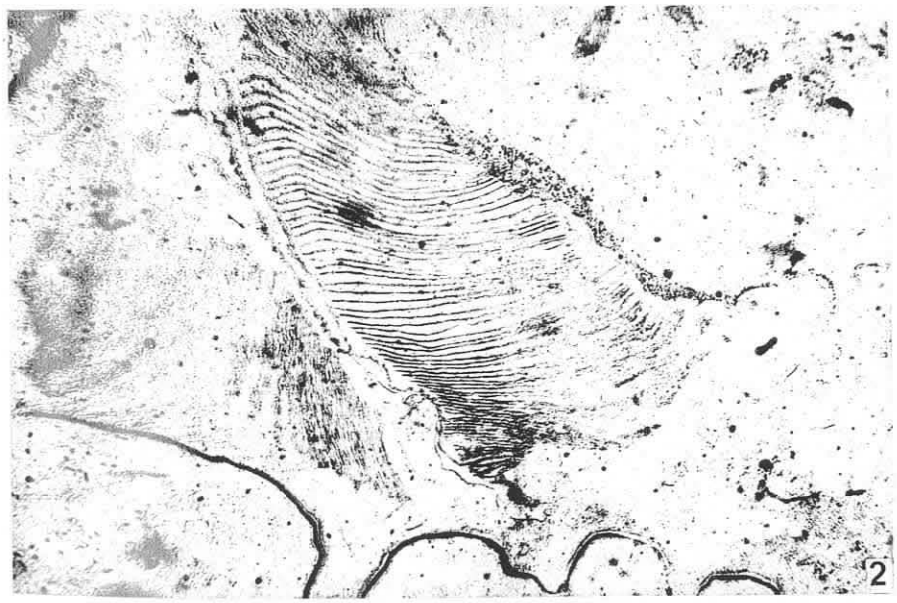
STORMER: Arthropods (myriapods and additional forms) from the Lower Devonian of Alken an der Mosel.

Plate 10.

Slides from the presumed Lower Devonian (Emsian ?) Rhynie Chert Bed; Aberdeenshire Scotland.

Figs. 1-2. Palaeocharinidae, g. et sp. indet. — Longitudinal sections of two book-lungs (photographs published in "Nature" by CLARIDGE & LYON 1961).
1. Specimen × 400.
2. Specimen probably × 400.





L. STØRMER: Arthropods (myriapods and additional forms) from the Lower Devonian of Alken an der Mosel.